OBSERVATIONS ON TRACHEARY ELEMENTS

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Introduction

Systematic studies of the secondary xylem of Angiosperms (*see* Tippo, 1946; Metcalfe & Chalk, 1950) have proved themselves to be extremely valuable in our understanding of the various cell types and cell arrangements from a phylogenetic point of view and have assisted greatly in adding more naturalness to current systems of classification. The efficient pursuit of these studies and also the effective use of the results were dependent on a complete, unambiguous, widely accepted, and objective system of descriptive terms. Studies of the tracheary elements of the early formed xylem have not yet reached this advanced stage, despite the fact that the literature on the subject is voluminous. Terminology has not been standardized, but often differs from author to author. Wherever terms such as "scalariform", "reticulate", and even "helical", "annular", and "pitted" are used without accurate descriptions and illustrations the meaning of the author is in doubt. Where the applications are made clear by appropriate illustrations, it is often found that the usages are highly variable. These generalities are made clear in the tables presented in the discussion at the end of this paper. Many citations were necessarily omitted from these tables because it was not possible to determine precise usages. In actuality, a large part of the material present in the literature in which tracheary elements are described is essentially lost to us through ambiguity.

The need for a relatively complete system of classification of the various types of tracheary elements is brought out by the great range in variability presented in the descriptive portions of this paper. Much of this variability would be obscure and relatively unusable if currently available, vague and all-inclusive terms were used to describe them. It is suggested from the present study and others mentioned below that there are several relatively distinct types of "reticulate" elements among the Angiosperms some of which may be restricted to certain families or groups of closely related families. The extent to which this statement is accurate is obviously dependent on future angiosperm survey type studies. Without proper specific terminology the distinctiveness of these "reticulate" elements is lost and hence the information is not usable. The recognition of certain types of simple reticulate and modified annular types adds significantly to an ultimate understanding of the relationships among some of the lower vascular plants. By proper description and terminology it is brought out that the Lycopodiaceae is probably very remote from the Selaginellaceae. Complete descriptions of early protoxylem elements of the ferns support previous suggestions that the Ophioglossaceae is relatively close to the Marattiaceae and that the Osmundaceae is closer to the above mentioned families than are any of the higher Filicalean families.

When walls are referred to as being lignified or unlignified the information is derived for the most part from sections stained with haematoxylin, safranin, and fast green or safranin and fast green only. The phloroglucinol-HCl reaction was used on several occasions on similar sections and was found to give the same results. Scarth *et al.* (1929) found correspondence between the phloroglucinol reaction and reactions with basic stains. Harlow (1928) indicates that deductions based on the phloroglucinol reaction must be taken with

reservation following the report of Crocker (1921) that phloroglucinol indicates only a particular portion of the lignin. Preston (1952) indicates that the phloroglucinol test is not specific for lignin. With the above indicated potential error in mind, the observations are presented. It is not the intent in this paper to characterize the primary xylem elements of all of the various plant groups included in this study. This is only too obvious from the very disproportionate sampling. The ultimate aim is a generalized concept of cell wall patterns and an interpretation of the more elaborate types of elements as well as the development of a usable system of classification of the various types of tracheary elements.

Materials and Methods

Sources of materials varied widely. Collections of both native and cultivated forms were made during the period from 1946 to 1959 in the vicinities of New Orleans, La., Minneapolis, Minn.; and Ithaca, N.Y. Living materials, especially ferns, were available in variety from the collections of the L.H. Bailey Hortorium and the Department of Botany at Cornell University and also the Department of Botany of the University of Minnesota. Preserved materials collected by J. Tilden in the Islands of the Pacific were available at the University of Minnesota as well as from the collection assembled by Professor A. J. Eames at Cornell University.

The following is a list of the species included in the study:

Psilotum nudum
P. complanatum
Tmesipteris tannensis
Lycopodium selago
L. obscurum
L. clavatum
L. lucidulum
L. complanatum
L. phyllanthum
L. cernuum
L. volubile
Phylloglossum dramondii
Isoetes engelmani
I. muricata
Botrychium virginianum
B. multifidum
B. dissectum
B. simplex
Ophioglossum vulgatum
O. pendulum
Helminthostachys zeylanica
Angiopteris evecta
Marattia alata
Danaea sp.
Osmunda cinnamomea
O. regalis
Todea hymenophylloides
Schizaea pusila
Anemia phyllitidris
Trichonomes sp.
Dicksonia sp.
Cibotium sp.
Dennstaedtia sp.
Pteridium aquilinum
Coniogramme japonica
Pellaea rotundifolia
Adiantum pedatum
Davalia fejiensis
Humata tyermanni
Nephrolepis exaltata
Pteretis nodulosa
Onoclea sensibilis
Dryopteris marginalis
Cystopteris fragilis
Blechnum sp.
Doodia maxima
Asplenium bulbiferum
A. trichonomes
A. viride
Scholopendrium sp.
Polypodium peroussum
Marsilea quadrifolia
Salvinia sp.
Cycas revoluta
Ceratozamia sp.
Dioon spinulosum
Ginkgo biloba
Taxus baccata (*sens. lat.*)
Cephalotaxus sp.
Araucaria excelsa
Taxodium distichum
Podocarpus macrophylla
Pinus mugho
P. banksiana
P. sylvestris
Picea abies
Tsuga canadensis
Larix laracina
Cedrus deodara
Cupressus sempervirens
Junipersus virginiana
Ephedra foliata
E. antisiphalitica
E. sp.
Welwitschia mirabilis
Gnetum leyboldii
G. schwackeanum
G. venosum
G. gnemon
Liriodendron tulipifera
Magnolia grandiflora
Michelia fuscata
Casuarina equisetifolia
Ligustrum vulgare
Hedera helix
Hibiscus esculentus
Citrullus vulgaris
Dracaena fragrans
Cordyline sp.
Aloe arborescens

Standard techniques of fixation, dehydration, embedding and staining were used. The most satisfactory staining procedure followed was one in which a combination of Heidenhain's haematoxylin, safranin, and fast green was employed.

A Note on Terminology

Early formed primary tracheary elements are often seen to have a relatively thin, continuous, unlignified first-formed wall and a relatively thick, discontinuous, lignified later-formed wall. Such a cell often enlarges or is stretched after com-

pletion of differentiation and maturation. During the stretching process, the first-formed wall is stretched. To this cell one can apply the terms primary wall (first-formed wall) and secondary wall (later-formed wall) with clarity and without ambiguity. The definition recommended by Bailey (1957) and more or less followed by Esau (1953) and by Eames & McDaniels (1947) in terms of stretchability is completely satisfied, as well as that apparently adhered to by Barghorn & Scott (1958) in terms of lignification. Similarly, the concept of Frey-Wyssling (1948, 1950) and Mühlenthaler (1950) of the primary wall as a very thin layer of cell wall deposited first is satisfied. And furthermore, the first-formed wall of the above described cell is comparable in many ways, although possibly not as thin, to the primary wall described by Preston (1952) in the wall of a tracheid from the secondary xylem of *Pinus*.

Among the extant vascular plants, the range in variation of early-formed primary xylem elements includes cells with:

(a) A thin, unlignified, continuous first-formed wall and a thicker, discontinuous, lignified later-formed wall;

(b) As in a, but portions of the later-formed wall are deposited on the first-formed wall at various times in the ontogeny of the cell; in addition, the later-formed portions of the later-formed wall may be either in strands or in sheets and may be deposited only onto the first-formed wall (and form pits!) or onto both the first-formed wall and the first-formed portions of the later-formed wall;

(c) As in a or b but first-formed wall is relatively thick and either lignified (after stretching) or unlignified, also it may become thick before elongation has ceased;

(d) As in a, b, or c, but later-formed wall showing various degrees and patterns of lignification, e.g. outer part of discontinuous wall unlignified (either continuously or discontinuously) and inner part lignified; or inner and outer part of discontinuous wall unlignified and middle part lignified; or patterns of lignification varying over different areas of cell;

(e) A thin, unlignified, continuous first-formed wall and a thicker continuous (except at pits) later-formed wall;

(f) As in e, but only the first-formed part of the later-formed wall is continuous, the inner part of the later-formed being discontinuous;

(g) As in e or f except lignification complete throughout wall (after stretching process is completed) or showing various degrees and patterns of lignification.

It seems clear that a working concept[1] of the primary and the secondary wall must be completely divorced from any consideration of lignification. It might be said that secondary walls are more often lignified than primary walls and that lignified walls are slightly if at all stretchable. But, nevertheless, lignification, it seems, must be regarded as an incidental secondary modification or else the entire usefulness of the concept of the primary and the secondary walls will be destroyed.

The usefulness of the terms is similarly imperiled if thickness or thinness is emphasized. Esau (1953) states that the primary wall may be very thin or relatively thick and multi-layered; whereas Frey-Wyssling (1948, 1950) and Mühlenthaler (1950) might restrict it to a very thin membrane. We are, to be sure, most familiar with the detailed structure of the very thin type of primary wall from recent studies with the electron microscope and less recent with polarized light; but this is no reason why this type of primary wall should dominate our concept. This would parallel the situation where the morphology of the Coniferales is described and thought of in terms of the Pinaceae (*sens. strict.*) or where the morphology of the ferns is described and thought of in terms of the higher leptosporangiate ferns, merely because certain genera are well known and occur in temperate regions in the vicinity of the larger universities[2].

The usefulness of the concept of the primary wall depends on its definition in terms of stretchability and correlated

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1. It is not the intent in this discussion to resolve or attempt to resolve the question as to whether or not there is a real and natural and consistent difference between the primary and the secondary wall, but to merely arrive at a workable concept. The terms in question have proven very useful in the past and it is quite improbable that they will be dropped from botanical usage in the foreseeable future.

2. This has been done!

submicroscopic structure, previous to secondary modifications such as lignification. If stretchability cannot be determined, the wall in question should be referred to as a presumed primary wall rather than a primary wall.

Descriptions of Some Tracheary Elements

LYCOPODIACEAE —*Lycopodium*: The first protoxylem elements to mature in the stem, root and leaf of *Lycopodium* are of a modified annular type. They are characteristic of the genus and are probably of diagnostic value. They are narrow, long elements occurring in groups of up to 20 or more cells (as seen in cross-section) with few or no intermixed parenchyma cells. The latter feature could probably be used to separate *Lycopodium* from all other extant vascular plants. The elements possess a delicate, unlignified primary wall with a series of annular thickenings on the inside. Adjacent rings are in turn interconnected by one or two vertically or obliquely oriented thickenings (Figs. 1-3). The interconnecting thickenings usually do not suggest helical bands between rings as are found in other groups such as angiosperms. Occasional rings are free from adjacent ones. In later formed elements of this type, the interconnections between adjacent rings are broader and more nearly vertically oriented (Fig. 4). The breadth of the interconnection may be so great that it appears as a sheet covering up to one-fifth of the surface area between adjacent rings. It is suggested that this type of element be called an *indirectly attached annular element*. This term would include elements found in the Lycopodiaceae, Equisetaceae, Marattiaceae, and Ophioglossaceae, each, however, with its own individuality.

The later formed protoxylem elements of *Lycopodium* possess a delicate, unlignified primary wall internal to which is a discontinuous system of thickenings in the form of a net (Figs. 6, 7). When this type of element is unstretched (Fig. 8), it might easily be confused with a helical element. The term *simple reticulate element* seems ideally appropriate in this instance. The forks and anastomoses (and consequently openings) in the early *reticulate elements* of *Lycopodium* are situated with only partial regard for cell faces and cell edges. The centres of the openings tend to be situated near the centres of the faces and therefore the forks and anastomoses tend to be in the vicinity of the cell edges. This is true even though the openings in the reticulum are broader than the faces and therefore overlap the edges.

There are elements which are somewhat intermediate in form between the *indirectly attached annular elements* and the *reticulate elements* (Fig. 5). There are no helical elements in *Lycopodium*.

In the transition from protoxylem to metaxylem in *Lycopodium* the discontinuous wall of the *reticulate elements* gradually assumes a more extensive nature (Figs. 9-11) with smaller openings which themselves gradually assume more extensive borders. The border, i.e. the overaching of the continuous wall by the discontinuous wall, is actually present to a degree in all of the tracheary elements of *Lycopodium* (Fig. 21). The openings, as well, become more and more restricted to cell faces, until toward the end of the transition, none of the openings intersect or cross cell edges and they are all essentially in uniseriate order on a given face and alternate with those on adjacent faces. At the end of the transition one finds openings in the inner wall which satisfy all criteria for bordered pits.

The pits are circular bordered in the narrower elements (Figs. 12-14) and elongate in the broader elements (Fig. 15). The elements with transversely elongate or scalariform pits follow ontogenetically those with circular bordered pits. Often scalariform pitting is absent, e.g. most stems of *L. selago*. Elements with circular bordered pits are regarded here as being at the same stage of phylogenetic specialization as those with scalariform pitting within the genus *Lycopodium*.

Lignification in the protoxylem and early metaxylem of *Lycopodium* is very sparse. The thickenings of the discontinuous wall possess an extensive unlignified (or very faintly lignified) core (Fig. 21, blackened area) with a relatively thin lignified covering. How much of the

discontinuous wall is truly secondary in the sense proposed by Bailey (1957) is difficult to determine, but this question will again arise below.

Phylloglossum — In conformance with the interpretation that *Phylloglossum* is a reduced form, the xylem elements of this genus are all of a relatively simple annular type (Figs. 16, 20). The elements possess a thin, unlignified primary wall internal to which are a series of thickenings in the form of rings which are usually lignified. The rings may occasionally fork (Figs. 16, 20, right side) or adjacent rings may occasionally be attached directly (Fig. 20, left).

Directly attached annular element is proposed as a descriptive term for elements with a series of rings which are attached to each other directly, not by means of interconnecting strands. This type of element has been found in *Equisetum* (Bierhorst, 1958), but here in *Phylloglossum* direct attachment is only occasional between pairs of adjacent rings. The term *simple annular element* is proposed for elements with a series of discrete rings without other elaborations.

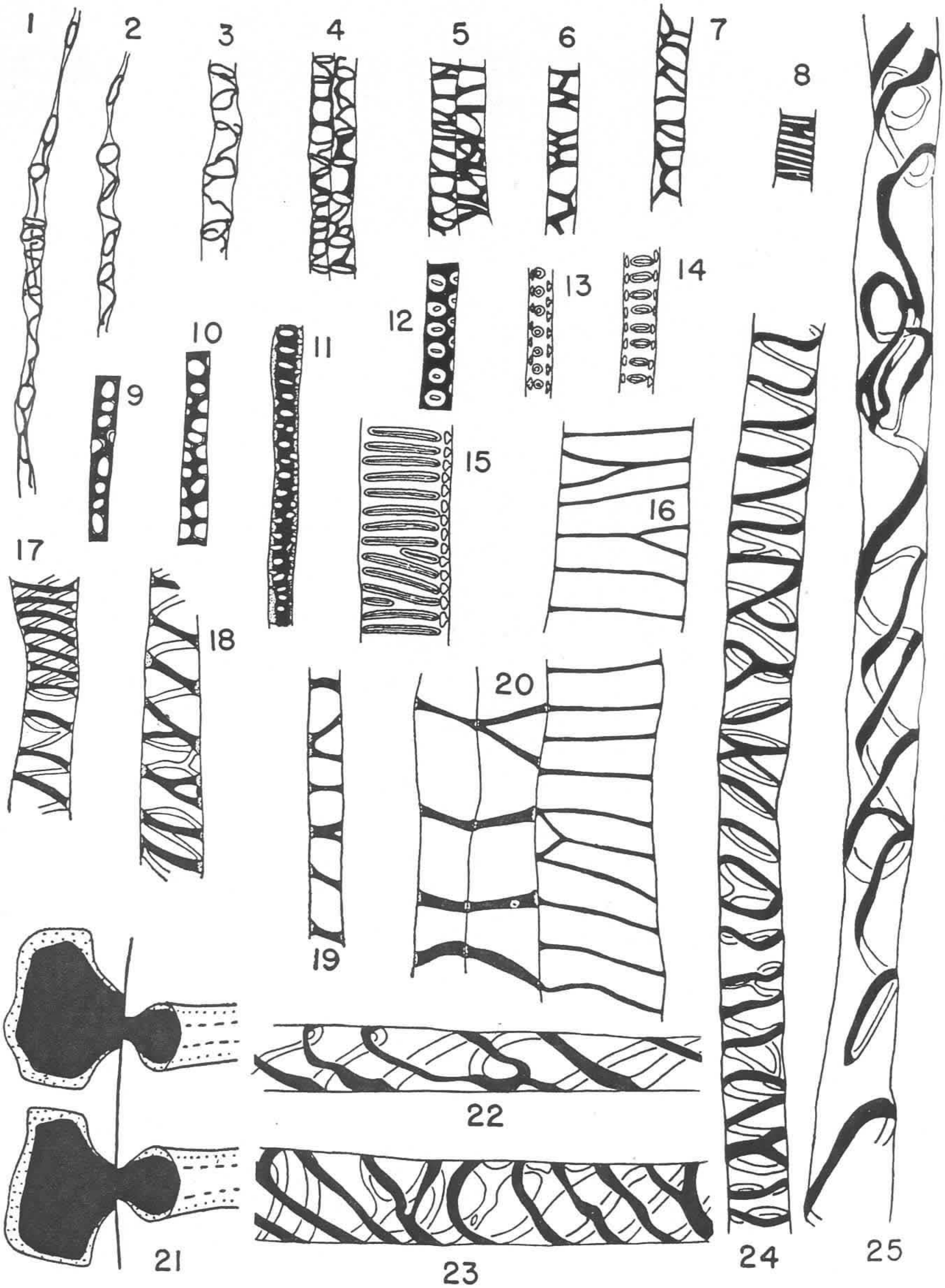
SELAGINELLACEAE—*See* Zamora (1958).

ISOETACEAE — Aside from the queer, isodiametric elements found in the "secondary" xylem of the corm of *Isoetes*, the xylem is entirely protoxylem and composed of annular and helical elements with some peculiarities. The annular elements possess a thin, unlignified primary wall and a series of lignified (often weakly) rings which may be forked or directly attached (Fig. 19) as in *Phylloglossum*. The later formed elements similarly have a thin unlignified primary wall and a lignified discontinuous wall. The discontinuous wall is often in the form of a simple, single helix (Fig. 18, upper part) through a large part of the cell or occasionally a pair of simple helices is present (Fig. 17, upper part). The helix or helices are rarely if ever continuous throughout a given cell, but end with a ring (Figs. 17, 18) with a new helix continuing from another ring. The double helix seems generally to end with a complete ring and not by a simple connection between the two (Fig. 169, bottom) or by blind endings of each of the two helices. The helical thickenings may be wound in different directions in different parts of the same cell in *Isoetes*, a feature known to occur elsewhere only in *Selaginella* (Zamora, 1958). Occasional forks and anastomoses occur in the helical elements of *Isoetes* (Fig. 18).

For convenience of description the following terms are proposed to describe helical elements. The term *simple helical* is proposed to describe elements which possess simple, unelaborated spiral thickenings. In addition the adjectives *single*, *double*, or *multiple* are added to complete the description of elements with one, two, or more individual spiral bands running parallel and independent of each other. The term *reversed helical* is proposed to describe elements in which the spirals are wound in different directions in different parts of the same cell.

Previous descriptions of tracheary elements of the lycopods are for the most part meager and uninforming, at least in the context of the present study, which for the most part concerns itself with highly specific characteristics of the type which were not of prime interest to previous workers. This, coupled with the facts that (1) descriptions of most primary tracheary elements have been presented as quite incidental observations to other anatomical studies; (2) descriptive terms for primary tracheary elements have been used in very ambiguous ways (*see* discussion) and without accurate illustrations it is often impossible to determine the way in which a given term is being used; and (3) interpretations of the overall patterns of thickening in tracheary elements are more often based on observations of one side of an element, e.g. unstretched simple reticulate elements are generally referred to as helical, makes it difficult to make full use of comments available in published literature.

The primary xylem elements of *Lycopodium* have been described as spiral followed by scalariform in the ontogenetic sequence (Campbell, 1928). Those of *Isoetes* as spiral or ring form (Ogura, 1938). The elements of several fossil forms have been described, e.g. LeClerc (1930) describes elements of *Stigmaria* as spiral and annular followed by barred



FIGS. 1-25.

elements, and Fry (1954) describes the elements of *Paurodendron* as annular, spiral and scalariform. The so-called Williamson's striations of the fossil lycopods will be discussed below (*see* discussion).

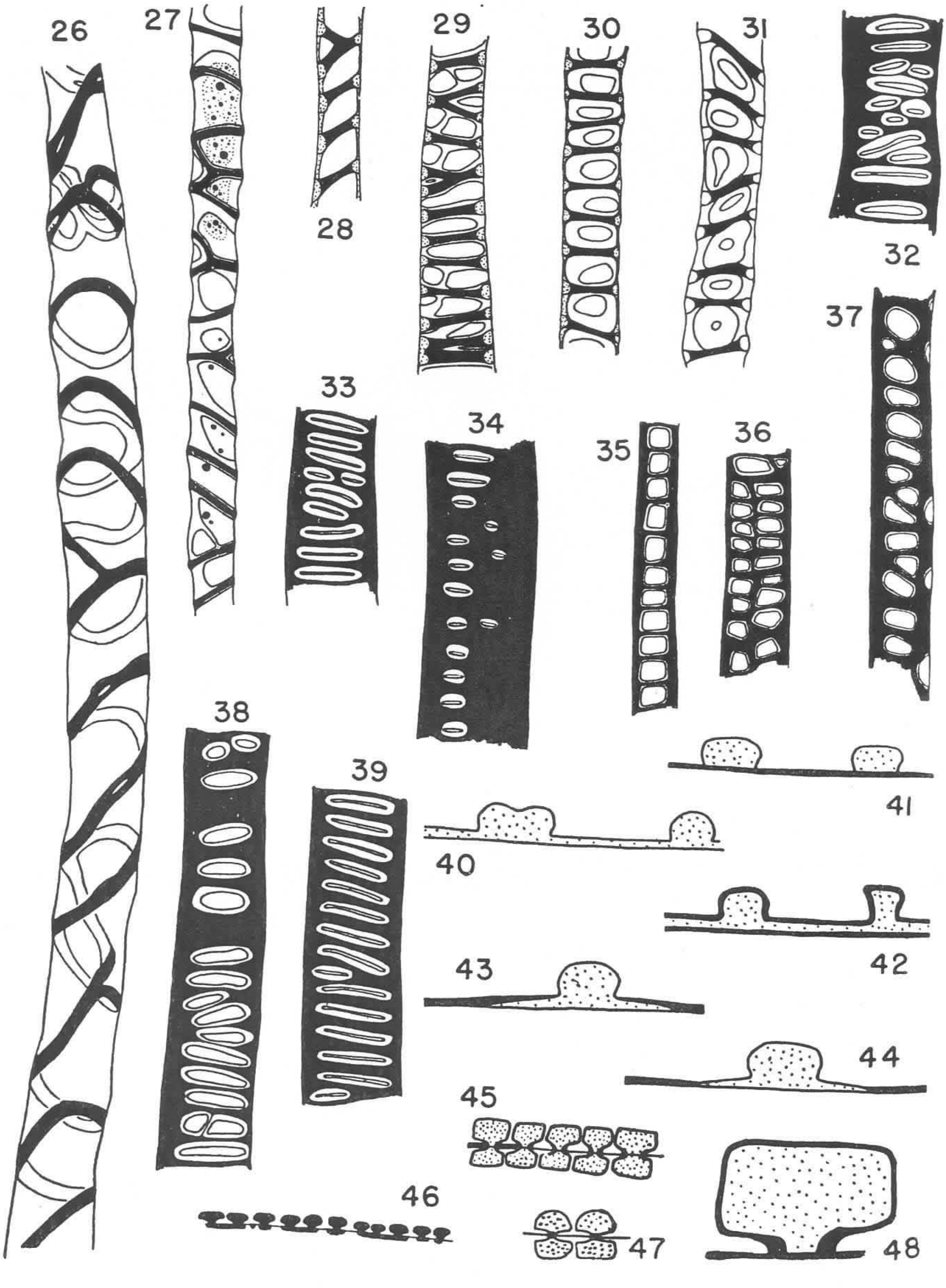
EQUISETACEAE — *See* Bierhorst (1958).

PSILOTACEAE — The first protoxylem elements to mature in the aerial stems (there is no protoxylem in subterranean stems) of the Psilotaceae are massive in size as compared to comparable elements of *Lycopodium*. This can be appreciated by comparing Figs. 22-27 with Figs. 1-7 all of which are reproduced at the same scale.

The early protoxylem elements of *Psilotum* and *Tmesipteris* are extremely similar if not essentially identical. They are similarly highly distinctive for the family. If, however, they are described as helical or annular-helical, their distinctiveness becomes lost. One can find in these elements (Figs. 22-26) some simple, unattached rings (Figs. 24, 26) as well as simple, unelaborated helical portions (Fig. 24, top, single helix; Fig. 25, centre, double helix). The helical portions terminate at a single ring (Figs. 24, 25), or with a dead end (Fig. 26, centre), or with a complex girdle (Fig. 26, top). Single helices often become double helices by a simple branching (Figs. 23, 25, 26). Annular thickenings may be directly attached to each other at an edge or they may be forked near their mid-sections (Fig. 24). Often small slit-like openings are found within a thickened band (Figs. 23, 26). These are not merely areas where the spiral thickening is slightly thinner than elsewhere, as in some other plant groups, but complete gaps in the thickening. The thickenings, both ring and helical, show a waviness or variation in width and seem not to fall along smooth curves, but to lay out a slightly sinuous path (Figs. 22-26).

In *Tmesipteris*, following ontogenetically the protoxylem elements are a series of distinctive reticulate elements (Figs. 35-37) with relatively large, often squarish, slightly bordered openings which are essentially all restricted to cell faces. In the progression of cell types (Figs. 35-39) the openings become less squarish, more spaced, more transversely elongate, and assume broader borders and narrower apertures, culminating in the later metaxylem with typical scalariform bordered pits (Fig. 39). This transition seems to be less gradual in *Psilotum* with reticulate-like elements less common. Elements similar to the one shown in Fig. 36 may, however, be found in *Psilotum* (*see* Fig. 9, in Moore & Andrews, 1936). Figures 32 and 33 represent portions of elements from the early metaxylem of *Psilotum*. Figure 34 shows a feature not uncommon in *Psilotum*, but extremely rare among non-seed bearing vascular plants. This is the presence of extensive areas of thick wall very sparsely pitted. In the figure, the three small pits on the right are on one cell face which abuts onto parenchyma, while the row of larger pits on the left are on another face which abuts onto another tracheid. In *Psilotum* the condition of sparse pitting is to be found only on walls common to tracheids and parenchyma.

FIGS. 1-25 — Figs. 1-4. Portions of early protoxylem elements from the stem of *Lycopodium obscurum*. × 666. Fig. 5. Portions of two adjacent elements of the intermediate protoxylem from the stem of *L. obscurum*. × 666. Figs. 6, 7. Portions of stretched reticulate protoxylem elements from the stems of *L. selago* and *L. obscurum*, respectively. × 666. Fig. 8. Portions of an unstretched protoxylem reticulate element from the stem of *L. obscurum*. × 666. Figs. 9-11. Portions of reticulate elements of the early metaxylem of the stem of *L. selago*, *L. selago*, bordered to scalariform pitted elements from the stems of *L. selago*, *L. obscurum*, *L. obscruum* and *L. obscurum*, respectively. × 666. Figs. 16, 20. Portions of tracheary elements from a new tuber and from the strolibus of *Phylloglossum*, respectively. × 666. Figs. 17-19 Portions of tracheary elements from the leaf trace of *Isoetes engelmani*. Figs. 18, 19 from the trace deep in the tissues of the corm. × 666. Fig. 21. Portions of the walls of two adjacent tracheary elements of the stem of *Lycopodium obscurum*. Protoxylem element on the right, metaxylem element on the left. Black represents unlignified wall; stippling represents lignified wall. × 7300. Figs. 22-25. Protoxylem elements from the aerial stem of *Psilotum nudum*. × 666.



FIGS. 26-48.

The pitting in the late metaxylem elements of the *Psilotaceae* can be described as uniseriate (Fig. 34), alternate or irregular (Fig. 32) on a given face and alternate across the cell edges from face to face. In shape the pits vary from circular bordered (Figs. 32, 38) to scalariform bordered. Elongate pits in a given element may be matched occasionally with horizontal pairs of pits in adjacent elements. In face view, such pit systems give the impression of elongate pits partly separated into smaller pits. It is difficult to determine from the illustrations of Moore & Andrews (1936, Figs. 6, 9) whether the apparently "dividing pits" are in reality what they are presented to be or merely face views of pit systems in which a single pit is matched with a pair of pits.

The application of the expression "transitional pitting" (Moore & Andrews, 1936) to the Psilotaceae will be discussed in a more general context.

The early protoxylem elements of both *Psilotum* and *Tmesipteris* first develop a thin, elastic primary wall then the characteristic lignified secondary thickenings. They may then loose their protoplasts and cease to change, save for being stretched passively. On the other hand, many, if not most, of the protoxylem elements produce more cell wall after the typical secondary thickenings are completely formed. This additional wall is deposited over the primary wall and either covers all or part of the area between the secondary thickenings. Figure 28 illustrates a portion of a protoxylem tracheid of *Psilotum* with the additional wall (shown in sectional view) covering the primary wall. In this instance the additional wall was complete and uninterrupted except at the secondary thickenings. For purposes of description and discussion it is essential that terminology be proposed for the additional wall. The term "tertiary wall" is obviously inappropriate because of its application in a different sense. The expression *secondary secondary wall*, although possibly a bit clumsy, seems appropriate.

The *secondary secondary wall* may be deposited as a sheet extending only a short distance outward from the thickenings of the secondary wall (Fig. 27), or it may be more extensive outlining simple pit-like areas between the secondary thickenings (Fig. 27, in part; Figs. 29, 30, 286). When these pit-like areas are well defined they tend to be restricted to cell faces and tend to avoid crossing cell edges. The pit-like areas are often squarish in outline and when restricted to cell faces give to the cell the aspect of the curious reticulate-like elements described above. Occasionally the secondary secondary wall is in the form of discs with a central aperture (Fig. 31), superficially resembling a series of bordered pits between the ordinary secondary thickenings.

Patterns of lignification in the tracheidal walls of the Psilotaceae are quite variable. These are shown in Figs. 40-45, 47, 48 where lignified wall is stippled and unlignified wall is blackened. In Fig. 40, a portion of the wall of the element shown in Fig. 26 is shown; here the entire wall is completely lignified. Figures 43 and 44 show other portions of the wall of the same tracheid of Fig. 26, where the helical thickening is lignified as well as the wall toward the outside and the wall adjacent to the thickening and extending outward from it. Figures 41 and 42 show portions of opposite sides of another protoxylem element where (Fig. 41, which is the side

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FIGS. 26-48 — Fig. 26. A portion of a protoxylem element from the aerial stem of *Psilotum nudum*. × 666. Figs. 27-31. Portions of protoxylem elements from the aerial stem of *P. nudum* showing the secondary-secondary wall. Structures in Figs. 30 and 31 are not bordered pits; *see* text. × 666. Figs. 32-34. Portions of metaxylem elements from the aerial stem of *P. nudum*. × 666. Figs. 35-39. Same from *Tmesipteris tannensis*. × 666. Figs. 40-45, 47, 48. Sectional views of portions of walls of tracheary elements of *Psilotum nudum*, showing patterns of lignification. Black represents unlignified wall; stippling represents lignified wall. Figs. 40, 43, and 44 are taken from various parts of the cell shown in Fig. 26. Figs. 41 and 42 are taken from opposite sides of the same cell. Figs. 40-44. × 2660. Figs. 45, 47. × 1330. Figs. 48. × 7990. Fig. 46. Sectional view of the wall of a metaxylem tracheid and adjacent parenchyma cell from the stem of *Tmesipteris tannensis*. × 666.

of the element bordering on parenchyma) the continuous wall is unlignified and the discontinuous wall is lignified and where (Fig. 42, which is the side of the element bordering on another tracheid) there is an outer and an inner layer of unlignified wall and a middle zone of lignified wall. Later formed metaxylem elements show a thin, unlignified primary wall on which the pitted wall is inserted. The thickening of the pitted wall, i.e. the portions between the circular bordered to scalariform bordered pits, may be entirely lignified except for a small ridge connecting them to the primary wall (Fig. 47) (*see* Esau, 1953, p. 229). The primary nature of this ridge will be discussed in connection with certain ferns below. There may be an unlignified zone on either side of the connection (as seen in sectional view), actually completely encircling the pit chamber (Figs. 45, 48). This is usually responsible for the sharpness with which the pit borders are seen in face view and may, in addition, give a false impression of a thickened pit-closing membrane if the focal plane is not carefully controlled (Fig. 45, left side). The unlignified areas bordering the pit chambers tend to thin out gradually from the primary wall inward and may even extend entirely over the wall surface (Fig. 48).

Pit matching between metaxylem tracheary elements and parenchyma often tends to be irregular in the Psilotaceae. This is shown in Fig. 46.

The tracheary elements of the Psilotaceae have been described as spiral in the protoxylem and scalariform in the metaxylem (Eames, 1936; Campbell, 1928; Ford, 1904). Annular thickenings were mentioned by Moore & Andrews (1936) and Ogura (1938).

MARATTIACEAE — The tracheary elements of the Marattiaceae show a number of peculiarities; none, however, are unique to the family. The earliest protoxylem elements (Fig. 49) have thin, unlignified primary walls and a secondary wall in the form of a system of rings interconnected by finer strands which are vertically or obliquely oriented. The interconnecting system between the adjacent rings in progressively later formed elements tends to become more extensive and here and there forms a limited reticulum (Fig. 50). The element shown in Fig. 49 is classified as a form of *indirectly attached annular element*. The term *annular-reticulate element* is proposed to cover elements in which adjacent rings are interconnected by a network of strands. This is not to be confused with the *reticulated annular element* in which the rings are distinct and unattached, but each one is in the form of a reticulum as occurs in *Equisetum* (Bierhorst, 1958). The more simple *indirectly attached annular element* shown in Fig. 49 was observed only in *Marattia* in the Marattiaceae; however, elements extremely similar to the element shown in Fig. 50 were seen in each of the three Marattiaceous genera studied. Portions of the *indirectly attached annular elements* and the *annular reticulate elements* suggest portions of helices, more so in *Angiopteris* than in either *Marattia* or *Danaea*. In the later formed protoxylem elements (Figs. 51, 52) strands of the reticula between adjacent major thickenings of the cells become progressively thicker until they are of the same magnitude as the major thickenings themselves. At this point the distinction between the two systems of thickening is lost and the cell must be described as a *reticulate element*. This transition appears more extensive in *Marattia* and in *Danaea* than in *Angiopteris*. In the later formed protoxylem *reticulate elements* of *Marattia*, in addition to the more typical meshes in the network, there are rarely present circular, distinctly bordered pits (Fig. 52).

The transition from protoxylem to metaxylem involves a shift in the relative positions of the forks and the anastomoses of the secondary network so that they tend to be associated with cell edges. The transition is not abrupt, but gradual, so that at first the openings in the network show a partial regard for cell faces and cell edges and later they are more or less entirely restricted to cell faces and do not cross cell edges. In a given portion of an element the openings may be entirely restricted to cell faces, while elsewhere on the same cell openings may cross cell edges. Figure 53 shows a portion of an element where the openings are restricted to cell faces; a cell edge is present running vertically down the centre of this part of the

cell. On the portion of the element shown in Fig. 54 the central row of openings and the two rows partially shown are essentially restricted each to a given face, but as can be seen, this is not as complete restriction as is shown in Fig. 55. Figure 60, on the other hand, shows what is merely a tendency toward restriction of openings to cell faces.

In the transition within the early metaxylem, the reticulate openings develop progressively broader borders and assume the form of typical scalariform bordered pits (Fig. 64). In *Angiopteris* even at this point in the succession one can occasionally observe incomplete restriction of openings to cell faces (Fig. 61).

In the tracheary elements of the Marattiaceae, as in several other groups, there is a small ridge of unlignified wall material between the typical thin primary wall and the secondary thickening (Figs. 58, 62). That this ridge is primary wall and can be referred to as the *primary ridge* seems fairly certain for the Marattiaceae, Osmundaceae, and certain angiosperms. In *Berberis* (Abbot, 1959) the ridge is formed before the tracheary element reaches maximum diameter; in other words, it is stretched laterally.

In *Angiopteris* (Fig. 56), at the points of branching within the reticulum of the early to late protoxylem, there is no direct or abrupt connection, but there is an extended groove beyond the point where two converging strands first touch each other (Fig. 57). The *primary ridge* is relatively pronounced in these elements (Fig. 58) and extends along the groove to a point beyond where the secondary thickenings separate (Fig. 58). When these elements are stretched there may be a sharp bend produced at the point of connection (Fig. 59) and/or the two converging strands may separate along the groove and thus stretch the *primary ridge* in a vertical direction.

That the primary ridge can be referred to as the morphological equivalent of the "Rim" or "Bar" of Sanio seems relatively clear from the work of Bailey (1919).

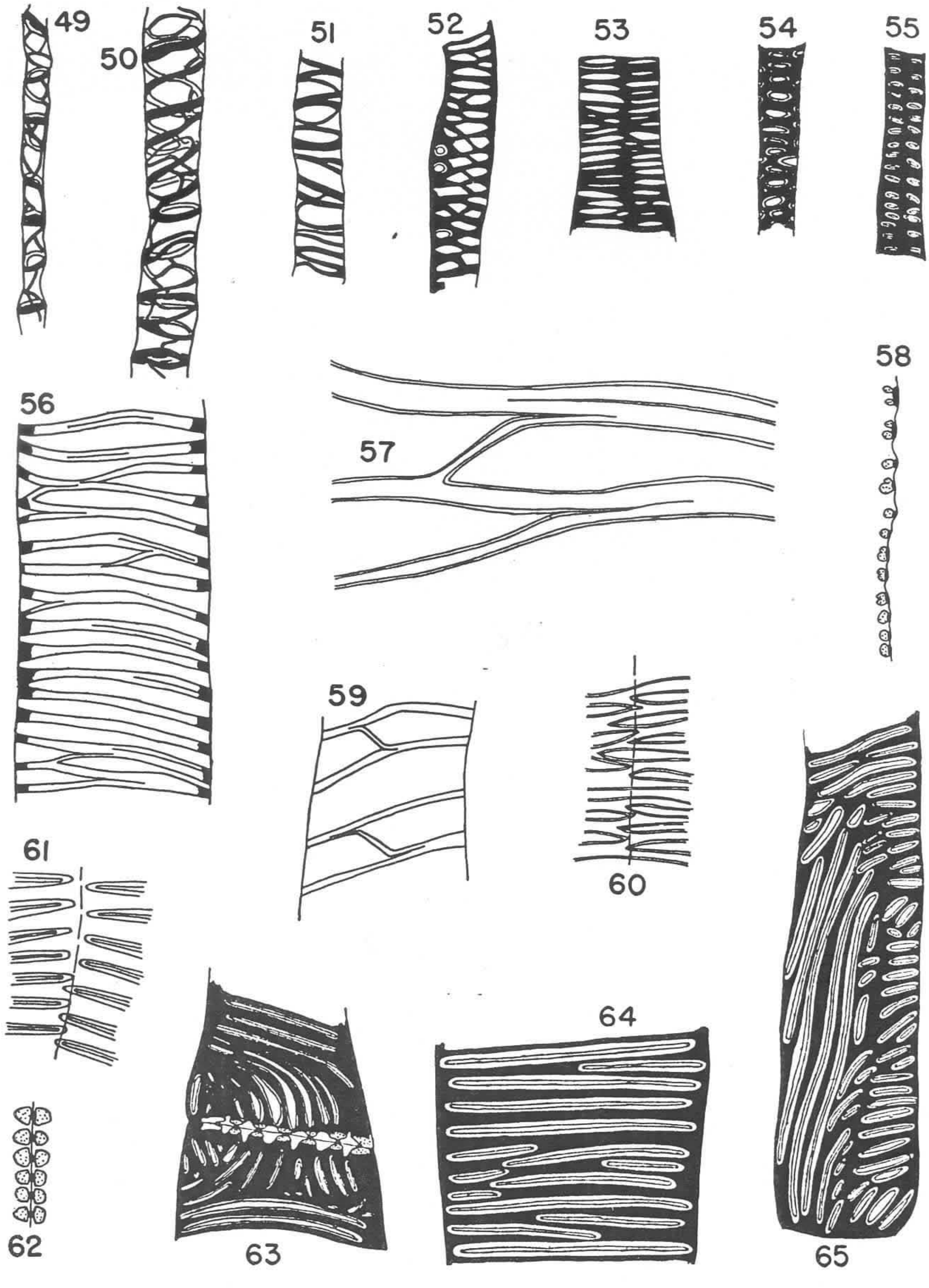
The scalariform bordered pits in the later metaxylem of the Marattiaceae alternate across the cell edges (Fig. 61). This is not surprising if essentially each one represents a single modified opening in a reticulum and their restriction to cell faces followed a sequence illustrated by Figs. 52, 60, 61. The term *trans-edge alternate pitting* is proposed to describe the pit arrangement described above and which similarly occurs in the scalariform elements of the Lycopodiaceae, Selaginellaceae, Psilotaceae, Cyacadaceae, and to some extent in the Osmundaceae. *Trans-edge opposite pitting*, on the other hand, is almost general among the higher leptosporangiate ferns and angiosperms.

Scalariform elements in which many of the elongate pits are oriented in a near vertical or lengthwise direction (Figs. 63, 65) have been observed in *Angiopteris*. This is generally associated with pitting in the opposing wall of the adjacent cell which is oriented in another direction. Or, in other words, the pitting is cross-matched. The opposing cell wall may have transversely or obliquely oriented pits. In *Angiopteris*, the *ob-scalariform pitting*, as it is proposed to call it, is more often near the end of a tracheid (Fig. 63), however, one can occasionally find such pitting elsewhere. Similar pitting has been observed in the Ophioglossaceae and in leptosporangiate ferns (*see* below). *Ob-scalariform pitting* is not to be confused with irregular reticulations which tend to occur in many plant groups in near isodiametric elements occurring near ends of vascular strands, e.g. leaf veins.

Tyloses frequently form in the protoxylem of the three genera of the Marattiaceae studied. In *Angiopteris* they are most extensive, eventually filling essentially all of the protoxylem elements and the earliest metaxylem elements. These have been referred to by McNicol (1908).

The tracheary elements of the Marattiaceae are generally referred to as being comparable to those of the Filicales (Eames, 1936; Bliss, 1939) with "typical" scalariform elements in the metaxylem.

OPHIOGLOSSACEAE — The early protoxylem elements of the Ophioglossaceae show striking similarities to those occurring in Marattiaceous genera. *Directly attached annular elements* occur in *Botrychium*, *Ophioglossum*, and also in *Helminthostachys*. The earliest elements of



FIGS. 49-65.

Botrychium (Figs. 66, 67) tend to have much finer thickenings than in comparable cells of *Ophioglossum* (Fig. 68) and *Helminthostachys* (not shown, but extremely similar to Fig. 68). *Directly attached annular elements* tend to grade into *annular-reticulate elements* and then into *reticulate elements* as in the Marattiaceae (Figs. 68-72).

Distinct helicoid thickenings occur in the Ophioglossaceae, but are quite uncommon. Elements with simple helical thickenings are entirely absent, but elements in which there is a helical band which is itself in the form of a reticulum do occur. Elements of this sort are here referred to as *reticulated helical*, not to be confused with *helical-reticulate* in which the reticulum is present between the gyres of a helix. In the more typical *reticulate elements* of the Ophioglossaceae a helical organization is often suggested.

In later formed reticulate elements of the Ophioglossaceae, openings in the secondary wall network usually do not tend to become restricted to cell faces. In *Ophioglossum* (Fig. 81) there is a trend toward reticulate elements with transversely elongate, slit-like openings and even towards openings (often of variable size and shape) with more or less distinct borders (Figs. 87, 88, 95). Scalariform elements of the type present in the Marattiaceae are, however, absent. Note the *ob-reticulate* arrangement of openings in Figs. 87 and 88. The element shown in Fig. 95 from the stem of *Ophioglossum vulgatum* represents the closest approach to the Marattiaceous type of scalariform element observed. In fact, only in the stem of this species was there observed a strong tendency for transversely elongate openings in a reticulum to be restricted to cell faces. These elements are illustrated and referred to as scalariform by Wright (1920, *see* her Fig. 7).

Distinctly bordered, more or less circular pits are a pronounced feature of the early and late formed tracheary elements of the three genera of the Ophioglossaceae. They are absent from the first formed protoxylem elements, but do appear in the protoxylem reticulate elements and later elements (Figs. 70, 71, 76, 77). In these elements there is a thick, unlignified primary wall, but the pit closing membranes are quite thin (Figs. 74, 78, 79, 80). The thick primary wall is clearly primary since it becomes thickened before the elements are stretched. The pit borders are usually formed by the lignified secondary wall; with the thickened primary wall not tending to overarch the pit chamber except to a very slight extent (*see* upper pit in Fig. 80). It seems justified to regard the thickened primary wall of the early tracheary elements of the Ophioglossaceae as the morphological equivalent of the "rims" or "bars" of Sanio, even though here it is in the form of a sheet and not a narrow bar or ridge. What is regarded as a comparable thickening in the Osmundaceae and in the Marattiaceae is mostly in the form of ridges on the primary base wall, but may fan out to some extent when secondary thickening strands unite.

In *Botrychium*, however, in the late protoxylem or early metaxylem pit pairs are present in which the base wall (presumed primary in this case) encloses the chamber (Fig. 82) and over which strands of the secondary thickening are present. A distinct border is formed by surrounding major thickenings of the secondary wall (Figs. 75, 82). Pit apertures in this could not be observed. In *Helminthostachys* a somewhat similar kind of a pit was observed, but without the extra

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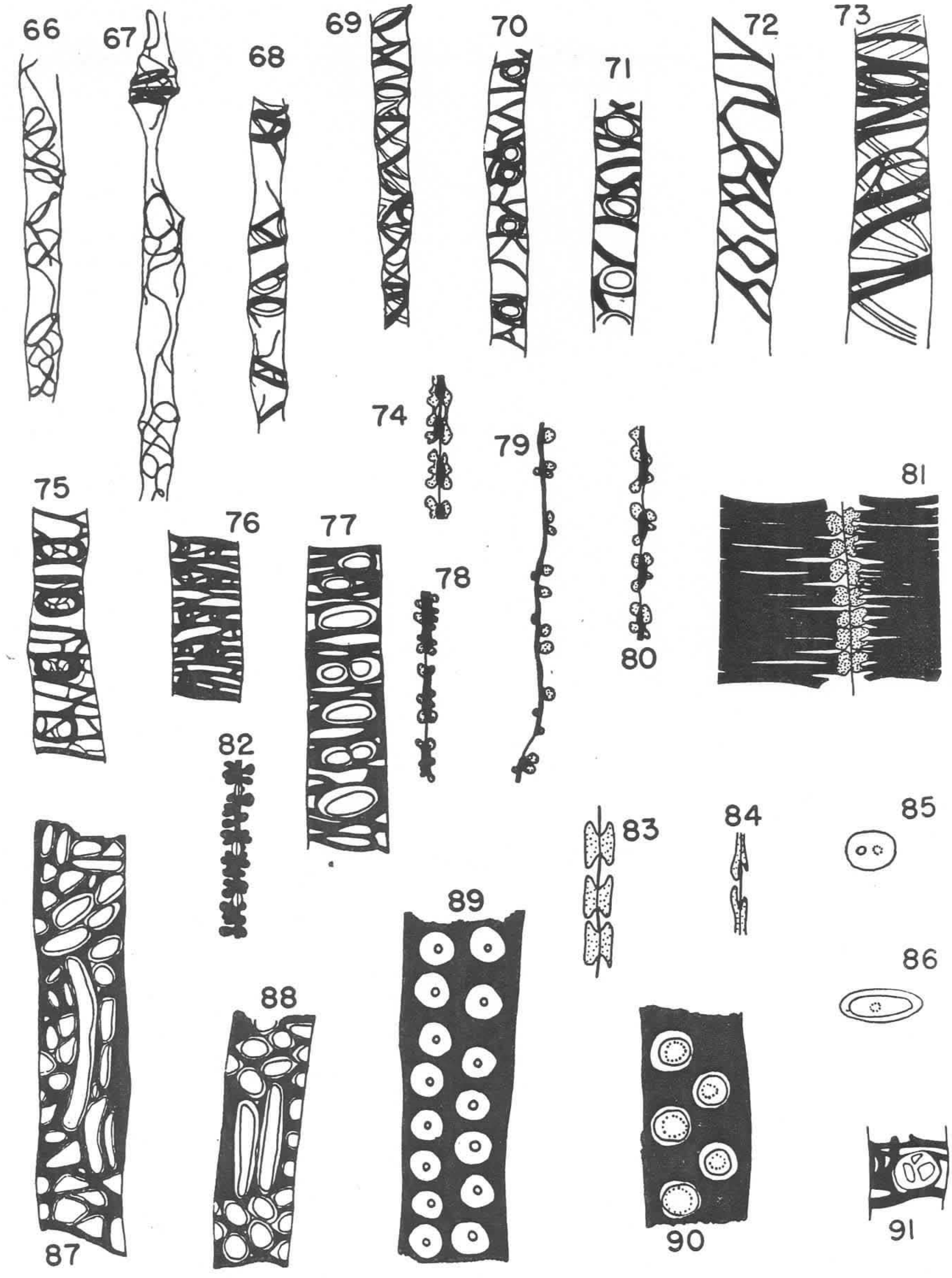
FIGS. 49-65 — Figs. 49-55. Portions of tracheary elements from the leaf of *Marattia alata*. × 666. Figs. 56-65. *Angiopteris evecta*. Fig. 56. Portion of a late protoxylem element. × 666. Fig. 57. Portion of Fig. 56 enlarged. Fig. 58. Sectional view of the wall of a late protoxylem element. × 666. Fig. 59. Portion of a late protoxylem element. × 666. Fig. 60. Portion of one of the latest protoxylem elements. This element is actually slightly stretched. × 666. Fig. 61. Portion of an element from the mid to late metaxylem. × 666. The broken line in Fig. 60 and in Fig. 61 represents a cell edge. Fig. 62. Sectional view of the walls of two adjacent scalariform elements. × 666. Figs. 63-65. Portions of scalariform elements from the metaxylem. × 666.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FIGS. 66-91.

strands of secondary wall material running over the outside of the chamber, and with several clearly defined apertures (Fig. 91).

The late metaxylem elements of the rachis of *Helminthostachys* show no more signs of reticulate structure, but merely a lignified secondary wall which is pitted in an alternate fashion (Figs. 83, 89, 90) on the inside of a very thin primary wall which is also lignified (except in the pit closing membranes) when the cell is matured. The opposing pit apertures of pit pairs in these elements are often of a very different size (Figs. 84, 86) and occasionally not in the center of the over-arching part of the secondary wall (Fig. 85).

The late metaxylem elements of the stems of *Botrychium*, *Ophioglossum*, and *Helminthostachys* and the " secondary " xylem of the stem of *Botrychium* characteristically show irregular thickening and often differential patterns of lignification in their secondary walls presenting some sort of reticulate pattern in face view (Figs. 92, 94, 97). In all three genera these elements possess a relatively thick unlignified primary wall (Figs. 93, 96, 98). The secondary walls of these elements in *Ophioglossum* tend to be uniformly lignified, but irregularly thickened on their inner surfaces (Fig. 98). The thickened, unlignified and differentially stained primary wall gives to the surface view a reticulate aspect with bordered pits between (Fig. 97). The pattern shown in black in Fig. 97 is interpreted as the system of " rims of Sanio ", shown in sectional view in Fig. 98. Differential thickening makes the pits in comparable elements of *Helminthostachys* appear to be in valleys within the secondary wall (Fig. 94). In *Botrychium*, both differential thickening and pronounced differential lignification are present (Fig. 93), again giving the face view of the element a strong reticulate aspect (Fig. 92).

The term " tertiary " wall has been applied to certain wall layers of tracheids of the three Ophioglossaceous genera (Wright, 1920; Loughridge, 1932). The term seems unnecessary and unjustified.

Considerable attention was given to the pit closing membrane in the Ophioglossaceae, since a torus has been reported to occur in each of the three genera (Wright, 1920). Occasional thickened membranes were observed in the stems of *Helminthostachys* and *Ophioglossum* and frequent ones in the stems of *Botrychium*, but membranes which were differentially thickened as in a torus were found only in *Botrychium dissectum* and here their occurrence was not constant. In view of these discrepancies in observations, it is possible that the torus within the family may be an eratically occurring feature.

In *Botrychium*, the unlignified primary wall, or more accurately the compound middle lamella, tends to be thicker around the edges of the pit chamber (Fig. 93, top; Fig. 100). This rim of thickened unlignified wall can be seen distinctly in face view of the pit (Fig. 99) and is considered

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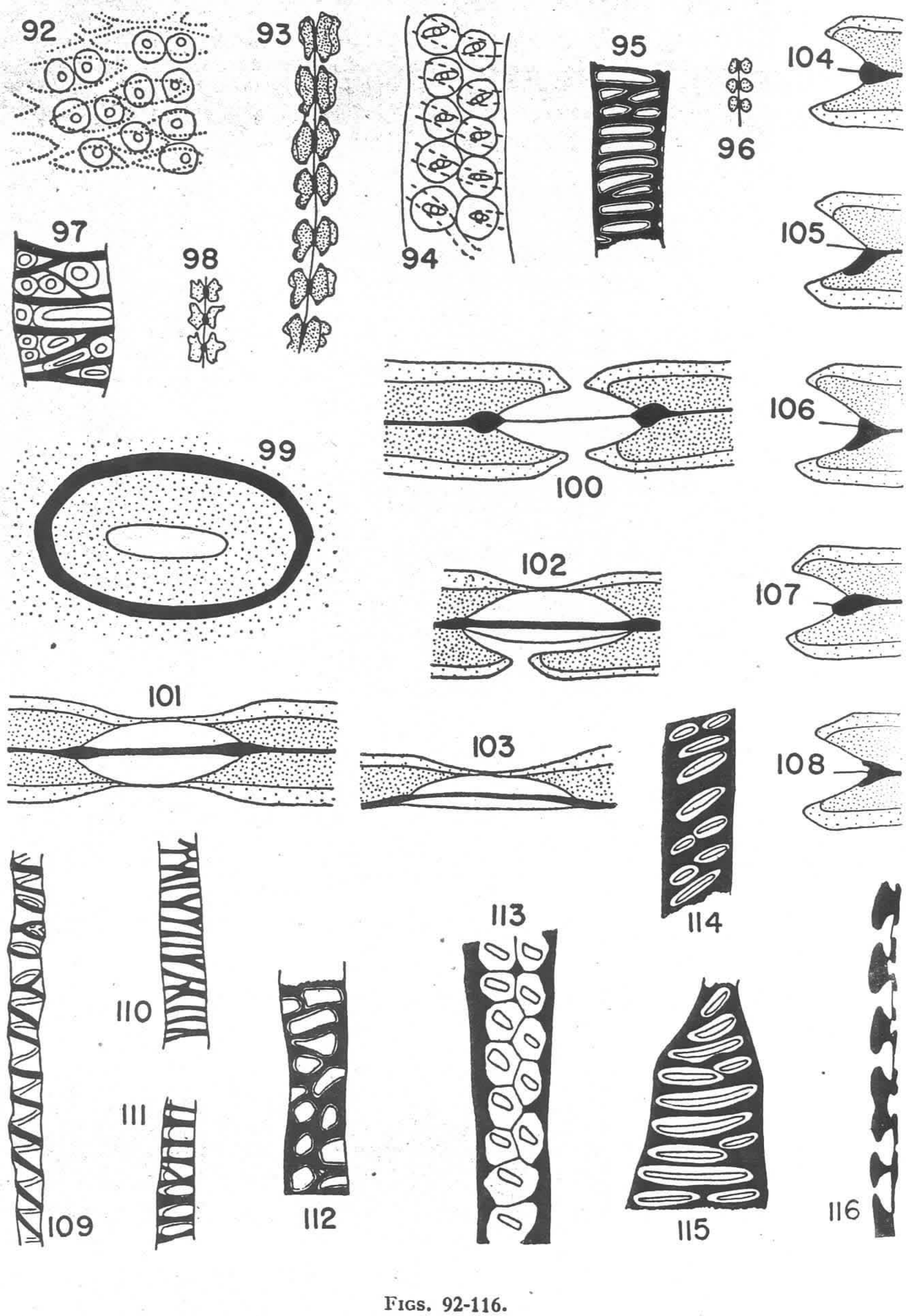
FIGS. 66-91 — Figs. 66, 67. Portions of tracheary elements from the petiole of *Botrychium multifidum*. × 666. Fig. 68. Same from the stem of *Ophioglossum pendulum*. × 666. Fig. 69, 70. Same from the petiole of *Botrychium multifidum*. × 666. Figs. 71, 72. Same from the leaf of *Ophioglossum vulgatum*. × 666. Fig. 73. Same from the petiole of *Botrychium simplex*. × 666. Fig. 74. As Fig. 73, sectional view of double wall. × 666. Figs. 75, 76. Portions of tracheary elements from the petiole of *Botrychium multifidum*. × 666. Fig. 77. Same from petiole of *B. simplex*. × 666. Figs. 78-80. Sectional views of portions of pairs of adjacent tracheary elements from the petiole of *B. simplex*. × 666. In Figs. 74, 78-80, stippled areas are lignified, blackened areas are unlignified. Fig. 81. Portions of two adjacent elements of the stem of *Ophioglossum pendulum*. × 666. Fig. 82. Sectional view of a portion of an early metaxylem element of *Botrychium multifidum*. × 666. Fig. 83. Sectional view of portions of walls of adjacent tracheary elements in the late metaxylem of *Helminthostachys* petiole. × 666. Figs. 84-86. Pit pairs in the late metaxylem of the petiole of *Helminthostachys* showing unequal opposing apertures. × 666. Figs. 87-88. Portions of elements in the metaxylem of the leaf of *Ophioglossum vulgatum*. × 666. Figs. 89-90. Same from the petiole of *Helminthostachys*. × 666. The dotted lines in Figs. 85, 86, and 90 represent the pit apertures of the opposing pits. Fig. 91. Portion of an element in the late protoxylem of the petiole of *Helminthostachys* showing a pit with three apertures and the pit truss. × 666.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FIGS. 92-116.

here as by Wright (1920) to be the morphological equivalent of the Rim of Sanio. Its shape in sectional view varies considerably (Figs. 104-108). It may appear as a symmetrical (Fig. 104) or an assymmetrical knob (Fig. 107) or it may extend outward and actually form part of the pit border (Figs. 105, 106, 108). It may even appear to extend slightly out onto the pit closing membrane (Figs. 100, 104, 107, 108). A sectional view of a pit pair at a non-median optical plane will show the unlignified rim suggesting a thickened pit closing membrane (Fig. 101). If the optical plane is slightly tilted both the rim and the true pit closing membrane may be seen (Figs. 102, 103). In the opinion of the author this is what is represented by the so-called " double membrane " of Wright (1920).

Tyloses occur in *Botrychium* and *Ophioglossum* in the early protoxylem. These have been referred to by McNicol (1908). They are not as extensively formed as in the Marattiaceae or in the Filicales.

The presence of bordered pits in the protoxylem elements of the Ophioglossaceae has been reported by Esau (1953). Nozu (1956), aware of Esau's report, could not recognize them in his material. The report of Esau was not particularly clear. She enumerated various plant groups in which bordered pits occur in protoxylem elements and indicated " and possibly Ophioglossales".

Loughridge (1932) described the protoxylem of the Ophioglossaceae as being composed of spiral and scalariform elements. Nozu (1956) reports the tracheids exhibiting spiral and scalariform markings on their walls " as in most ferns". Halle (1875) describes *Botrychium* as possessing spiral, netted to " leiterförmig ", and bordered pitted elements and *Ophioglossum* as having mostly "leiterförmig" elements. Farmer & Freeman (1899) reported in *Helminthostachys* the presence of tracheids with bordered pits, oval or almost circular, and also tracheids " in which the pits assimilate the more scalariform type met with in other members of the family." Petry (1914) described from *Ophioglossum pendulum* elements with spirally and reticulately thickened walls.

OSMUNDACEAE — The early elements of the Osmundaceae show some similarities to those of the Ophioglossaceae and the Marattiaceae. The earliest elements are annular with some interconnections (Figs. 117, 118, 125). The interconnections are of approximately the same thickness as the rings themselves and they more often suggest portions of helices than corresponding elements of the Ophioglossaceae. In the stem, succeeding elements (Figs. 119-121) strongly suggest Ophioglossaceous and Marattiaceous types save for the absence of bordered pits. Compare Fig. 119 with Figs. 50 and 69. Figure 119 is a reticulate element, still with some suggestion of rings here and there. The later elements shown in Figs. 120 and 121 are protoxylem reticulate elements. In the

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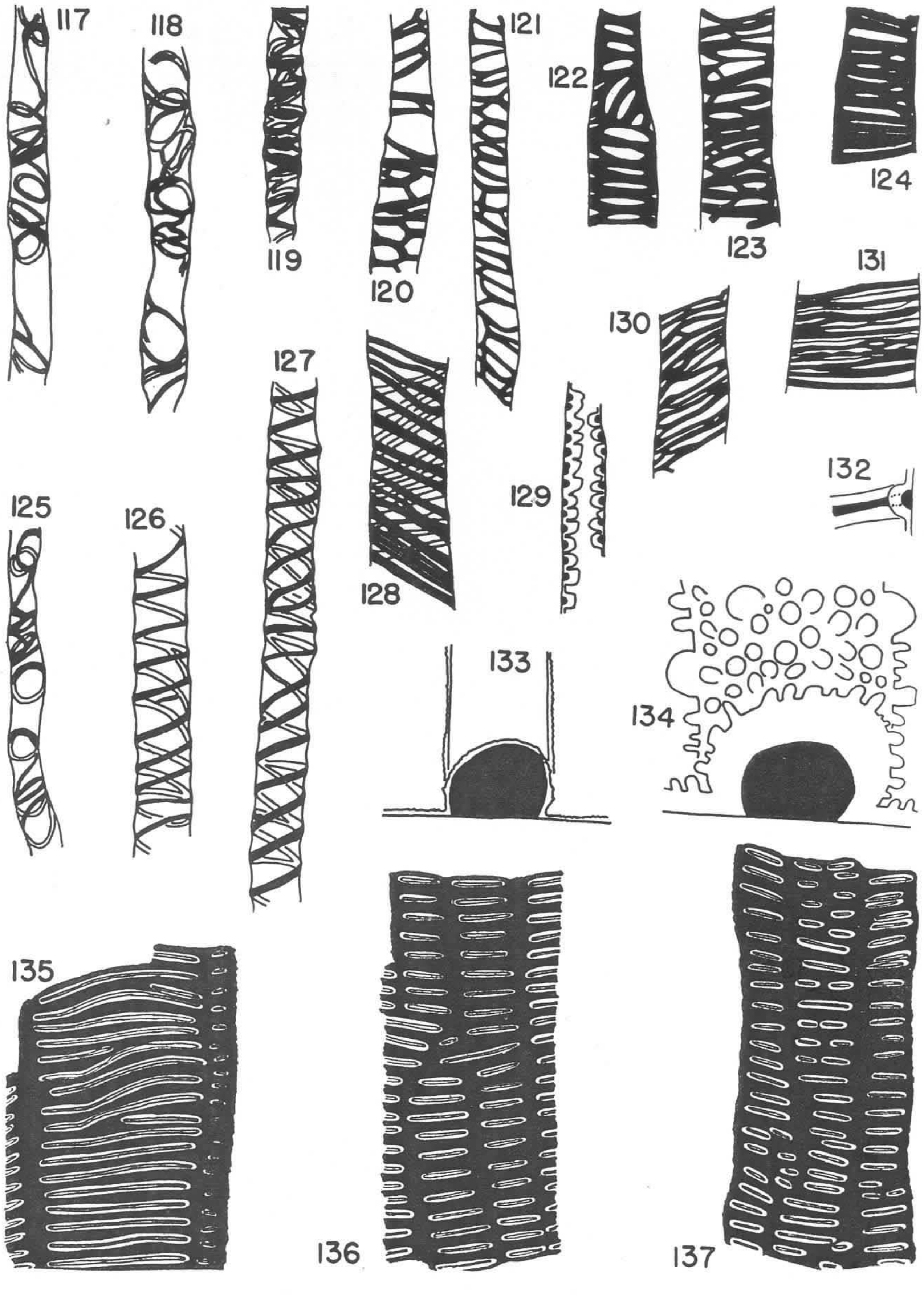
FIGS. 92-116 — Fig. 92. Portion of an element from the late metaxylem or " secondary " xylem of *Botrychium virginianum*. Fig. 93. Same as Fig. 92, but sectional view of wall and opposing wall. Fig. 94. Portion of an element of the late metaxylem of the stem of *Helminthostachys*. Fig. 95. Same from the stem of *Ophioglossum vulgatum*. Fig. 96. Sectional view of the wall of the element shown in Fig. 95 and the opposing wall. Fig. 97. Portion of an element of the metaxylem of the stem of *Ophioglossum vulgatum*. Fig. 98. Sectional view of a part of the wall of the same cell as shown in Fig. 97, and the opposing wall. Figs. 99-108. *Botrychium virginianum*, " secondary " xylem. Fig. 99. Face view of a pit. Fig. 100. Sectional view of a pit pair, median optical. Fig. 101. Sectional view of a pit pair, non-median optical. Fig. 102. Sectional view of a pit pair, slightly oblique orientation with respect to optical plane. Fig. 103. Sectional view of a bordered pit and the adjacent primary wall of a parenchyma cell, slightly oblique orientation with respect to optical plane. Figs. 104-108. Sectional views of the edges of pit pairs. In Figs. 93, 96, 98, and 100-108, the blackened areas are unlignified, the densely stippled areas are weakly lignified, and the less densely stippled areas are strongly lignified. The dotted network shown in Fig. 92 indicates the face view appearance of the inner, strongly lignified parts of the wall shown in Fig. 93. Figs. 109-116. Elements of *Cycas revoluta*. Figs. 109-111. Taken from young leaf raches. Figs. 112-116. Taken from the axis of a " bulb " or adventitious shoot. Figs. 92-98, 109-116. × 666.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Figs. 117-137.

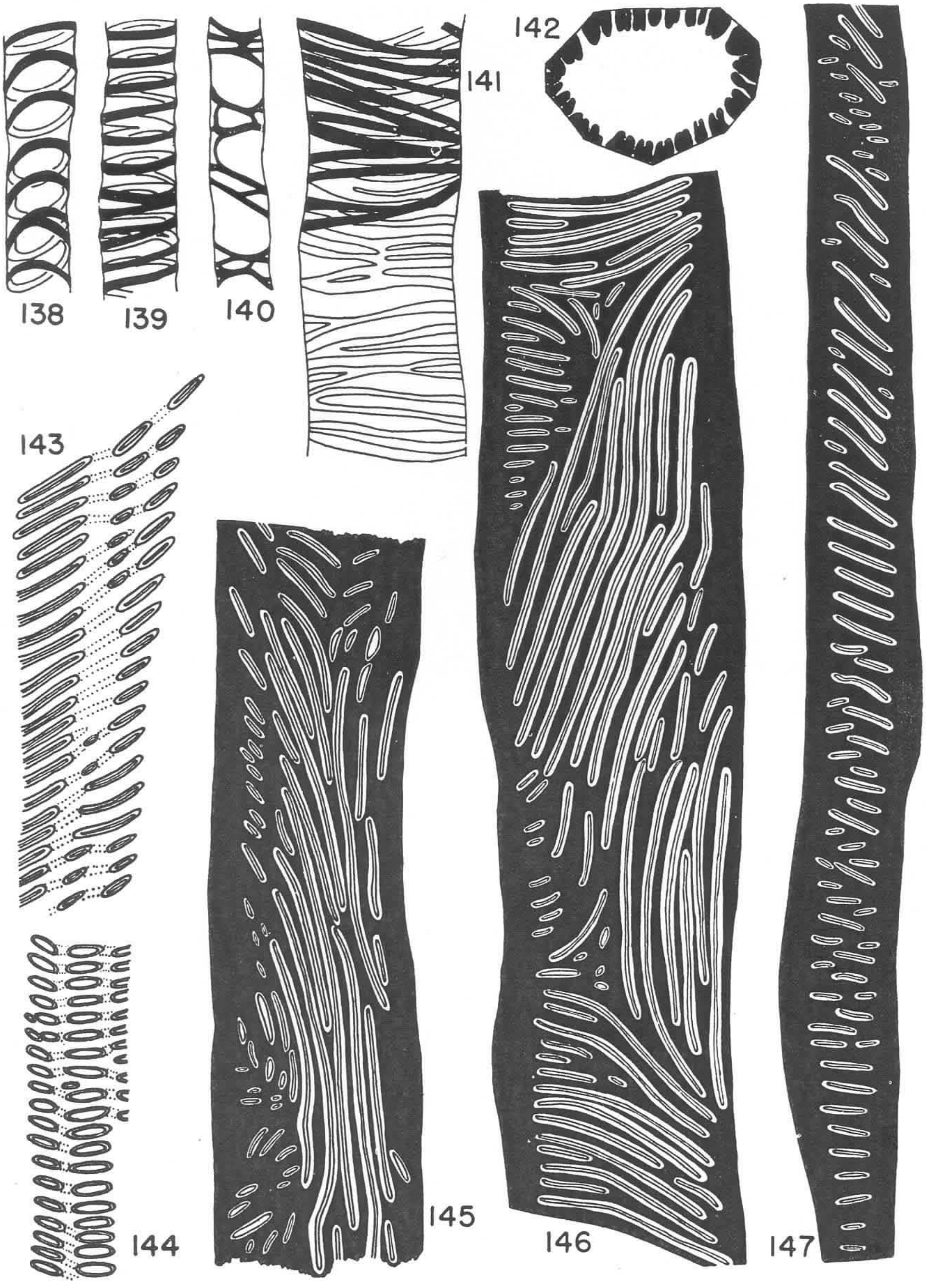
leaf, on the other hand, the helical pattern is well expressed (Figs. 126-128). The helical thickenings are relatively simple, but are single here, double there, and still multiple elsewhere, as the bands divide and recombine. There are, however, in the early helical elements few or no anastomoses between adjacent gyres. In other words, the elements may be stretched out, their helices uncoiled without rupturing any of the secondary strands. Occasionally several distinct and separate helical thickenings will run parallel for a distance in a given element (Fig. 128). Later helical elements in the protoxylem appear reticulate in face view (Fig. 130, 131), but are really helical in gross organization. In addition to forks, there are also a few anastomoses.

For describing the simpler types of helical elements the following nomenclatural proposals are presented: A *fork* in the helical system is intended to refer to a branching of a helical band to produce two helical bands. An *anastomosis* is intended to mean an interconnection between adjacent gyres, or in other words, a strand which would necessarily rupture if the helical system were to be stretched sufficiently. When viewing one side of an element, the *forks* are not distinct from the *anastomoses*; the distinction becomes apparent only when the three dimensional aspects of the helical system are taken into account. The term *singly helical* is meant to describe elements with a single helical band, similarly *doubly helical* for elements with two such bands, and *multiple helical* for those with more than two. The expression *singly-doubly helical* is presented to describe an element in which the helix is single at one point then forks to become double then recombines to become single again. The latter type of helical element occurs in its most diagrammatic form in each of the three Gnetalean genera.

The transition from early reticulate to scalariform in the Osmundaceae is similar to that in the Marattiaceae. Some differences, however, deserve to be mentioned. The early reticulate elements are essentially identical in both families. As will be seen below, the same comparison can be made with the early reticulate elements of the higher Filicales. In the later reticulate elements of *Osmunda*, the restriction of openings in the network to cell faces is long delayed and even in the last formed scalariform elements it is incomplete, so that both trans-edge alternate and trans-edge opposite pitting are to be found (Figs. 135-137). A considerable amount of heterogeneity is to be found in the intermediate reticulate elements; that is, thickenings of various sizes, some rather thin as compared to others (Figs. 123, 131). Figure 131 is actually a helical element, but it illustrates the kind of heterogeneity also found in some of the reticulate ones. Interconnections between converging strands usually show the extended groove which tends to separate on stretching of the element as in the Marattiaceae.

Patterns of lignification in early elements deserve mention. The earliest elements of the Osmundaceae show the annular or helical thickenings with a pronounced unlignified core which is overlain with a thin lignified wall which is continuous not only over the thickening, but also over the continuous base wall. Its inner surface tends to be somewhat irregular (Fig. 133). In the later protoxylem elements the inner lignified wall is more massive and its irregularities are accentuated (Fig. 134). There is a slight border (overarching),

FIGS. 117-137 — Portions of tracheary elements of *Osmunda cinnamomea*. Figs. 117-124, 135-137, from stem. Figs. 125-134, from leaf. Figs. 117-131, 135-137. × 666. The element shown in Fig. 129 is a helical element. The sections through the gyres are shown in black and were lignified. The inner wall shown clear was unlignified. Fig. 132 is a portion of a helical thickening from another element showing a lignified core (blackened area). Fig. 133 is a portion of a helical thickening from one of the earliest protoxylem elements, again showing a lignified core (blackened area) and slight irregularities on the inner, unlignified wall. Fig. 134 is the same as Fig. 132, but enlarged and with additional details of wall irregularities shown. Figs. 133 and 134 are reproduced at the same scale.



FIGS. 138-147.

but a pronounced false border due to the unlignified core (Fig. 132).

Tyloses occur in the protoxylem of the Osmundaceae (Figs. 163, 165) as in families previously mentioned. The tyloses often enter one tracheid from adjacent parenchyma, expand and extend into yet another tracheid (Fig. 165) as described by McNicol (1908). The tyloses in *Osmunda* as well as in many other ferns extend into a protoxylem element between two adjacent thickenings and are thus restricted by the secondary thickenings on two sides only, but in cross-section the young tyloses are still circular (Fig. 163), not broadly eliptical as one might expect.

Previous references to the structure of the tracheary elements of the Osmundaceae are few and relatively uninforming. Faull (1901) refers to two kinds of wood elements in the family: small ringed and spiral elements in the protoxylem and scalariform tracheids in the metaxylem. Bliss (1939) ascribes to the Osmundaceae elements not markedly different from the fern genera with scalariform pitting and occasional " serial pitting ".

HIGHER FILICALES — It seems pointless to discuss the tracheary elements of the Filicales family by family in view of the nature of the sample selected for this study. The " higher Filicales " as used here refers to all of the families of the order except the Osmundaceae. The sample taken might be considered highly inadequate to characterize the group, however, the constancy with which certain characteristics are observed from genus to genus permits a limited amount of justified generalization. In addition, the information collected during the examination of the members of this rather meager sample will add materially to an overall interpretation of certain aspects of tracheary element morphology.

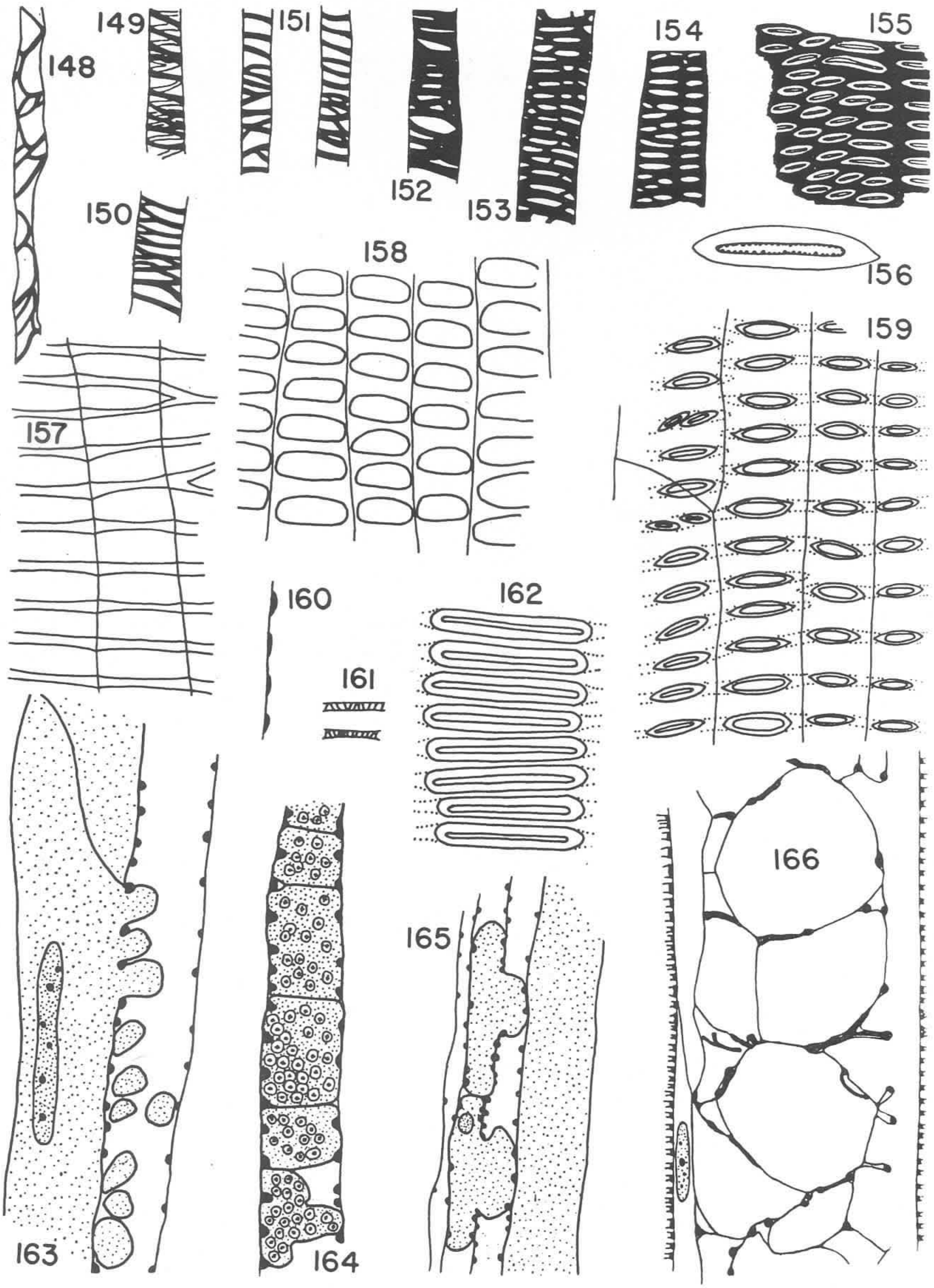
Copeland (1947) in his *Genera Filicum* recognizes 18 families in addition to the Osmundaceae in the order Filicales. Of these 18, 11 are included in the present study. The 25 genera and 27 species (*see* Materials and Methods) studied are distributed among the 11 families as follows:

Schizaeaceae, 2 gen. and 2 spp.; Hymenophyllaceae, 1 gen. and 1 sp.; Pteridaceae, 7 gen. and 7 spp.; Davalliaceae, 3 gen. and 3 spp.; Cyathaeaceae, 1 gen. and 1 sp.; Aspidiaceae, 4 gen. and 4 spp.; Blechnaceae, 2 gen. and 2 spp.; Aspleniaceae, 2 gen. and 4 spp.; Polypodiaceae, 1 gen. and 1 sp.; Marsileaceae, 1 gen. and 1 sp.; Salviniaceae, 1 gen. and 1 sp.

In the early protoxylem of the stems and raches of the higher Filicales, one typically finds loosely reticulate elements (Figs. 140, 148) similar to those found in the Osmundaceae. In the stems these elements are more often the first to mature. In leaves, however, they are preceded by annular and helical types. The annular elements when present occasionally possess an extensive series of simple separate rings, e.g. in the rachis of *Pteridium*, but more often are in part helical (Figs. 138, 139). Helical elements usually follow in the ontogenetic sequence the annular or annular-helical hybrid types, or they may be the first in the sequence. The helical elements are rarely if ever as diagrammatically simple as they often are in certain angiosperms, but possess rather frequent forks (Figs. 139, 149), and in the latter members of the helical series, anastomoses (Figs. 150, 151). In Fig. 151 opposite sides of the same cell are shown. It is clear that in the upper part of the portion of the tracheid shown the helix is simple, but toward the lower end forks and anastomoses produce a reticulate effect.

The protoxylem elements of most of the higher Filicales in the later ontogeny of the organ possess tyloses (Figs. 164, 166). The tyloses are often compound (Fig. 166), that is, they enter a tracheid from a

FIGS. 138-147 — Figs. 138-144, 146, 147. Portions of tracheary elements of *Blechnum*. Fig. 142 is a cross-section of an element similar to the one shown in Fig. 146. The dotted lines in Figs. 143 and 144 indicate the continuity of thinner areas across cell edges, i.e. the valleys in which the pits are situated. Fig. 145. A portion of an element from the stem of *Dennstaedtia*. All × 666.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FIGS. 148-166.

parenchyma cell then enter another tracheid from the first one. This may be repeated several times as described by McNicol (1908). The tyloses often, especially in *Pteridium* raches, enlarge considerably and completely distort the region of the protoxylem (Fig. 166). A cross-section corresponding to Fig. 166 usually shows what appears to be several large "parenchyma cells" which is the "cavity parenchyma" of McNicol (1908). In the rachis of *Pteridium* the cavity parenchyma occupies a larger area than did the protoxylem since the tyloses form and enlarge before the surrounding tissues have fully expanded laterally. Gwynne-Vaughan (1908) who considered most fern tracheids to have lateral perforations rather than pits quotes Weiss (who reported tyloses in *Zygopteris* and *Rachiopteris*, Weiss, 1906) from her personal communications as saying that the presence of open passages in the side walls renders it easy to account for the tyloses he found far away from any living elements. In all instances in the present study the membranes were clearly observed. Weiss (1906) used the presence of tyloses as "confirmatory evidence" to indicate two petrified fern specimens, a stem and a rachis, were connected. In view of the almost general occurrence of tyloses in the early primary xylem of ferns this now seems quite unjustified. Molish (1888) described tyloses in a great variety of vascular plants, but could not detect them in any of the ferns which he examined; he however, studied only late metaxylem.

It will be recalled that in the Ophioglossaceae and in the Marattiaceae, the protoxylem elements show a large amount of heterogeneity in the thickness of the secondary thickenings within given cells as regards to a face view appearance of the cells. This kind of heterogeneity is expressed to a much lesser extent in the Filicales, with the Osmundaceae and the Schizaeaceae showing the greatest amount in the order. In *Schizaea* the heterogeneity is pronounced not only in a face view aspect (more accurately the width of the thickening), but also in the dimension along the radius of the cell (the depth of the band). In this genus the feature is expressed not only in the protoxylem, but also into the late metaxylem where a face view of a scalariform element at a given focal plane will give the impression that certain of the transverse bars are unattached at one or both ends to the rest of the secondary wall. Outside of the Osmundaceae and the Schizaeaceae within the Filicales, heterogeneity is unpronounced, but usually can be detected.

The ontogenetic sequence of tracheary types in the higher Ficales thus far described is (1) annular (or annular-helical), (2) helical, (3) loosely reticulate with either 1, 2 or 1 and 2 omitted from the sequence. The reticulate series which follows is somewhat similar to that found in the Osmundaceae (Figs. 141, 152, 153, 154). Complete restriction of openings in the reticulum to cell faces is not common in the higher Filicales. Occasionally one finds

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FIGS. 148-166 — Figs. 148, 150. Portions of tracheary elements from a young rachis of *Scholopendrium*. Figs. 149, 151. Same from stem of *Polypodium peroussum*. Figs. 152-154. Same from rachis of *Asplenium viride*. Fig. 155. Same from young rachis of *Onoclea sensibilis*. Fig. 156. One pit enlarged from Fig. 155. Figs. 157-159. Stages in the development of the wall of a vessel adjoining parenchyma cells of *Pteridium aquilinum*. The vertical lines may be considered to represent the edges of the vessel wall or the junctions between adjacent faces or sectional views of the walls of adjoining parenchyma cells the planes of which are at right angles to the plane of the paper. Fig. 160. Sectional views of the thickenings shown in Fig. 157. Fig. 161. Face view of two of the thickenings shown in Fig. 157 showing pattern of differential staining. Fig. 162. Portion of an element from the rachis of *Pteridium aquilinum*. The dotted lines represent the continuations of the valleys of the wall in which the pits are situated. Fig. 163. Portions of two parenchyma cells and an adjacent protoxylem element with a number of tyloses from the leaf of *Osmunda cinnamomea*. Fig. 164. A portion of a protoxylem element filled with tyloses from the stem of *Onoclea sensibilis*. Fig. 165. Tyloses in the protoxylem of *Osmunda cinnamomea*. Fig. 166. The protoxylem of an old rachis of *Pteridium aquilinum* completely disrupted by tyloses. Figs. 148-155, 157-166. × 666.

toward the end of the reticulate series elements in which the openings do not cross cell edges, but are trans-edge opposite (Fig. 154) · This will be discussed below.

Scalariform elements with trans-edge opposite pitting seem to be of general occurrence among the higher Filicales. Trans-edge opposite pitting always occurs along with at least some trans-edge alternate pitting. This is observed with at least the same frequency as discontinuities are observed in the transverse rows of pits on the faces (if there is any opposite pitting on the faces) or with at least the same frequency as elongate pits end on the faces and are not opposite to adjacent ones. More often the frequency of occurrence of trans-edge alternate pitting in elements which are described here as having trans-edge opposite pitting is somewhat higher than the frequency of occurrence of row disturbances on the faces. This indicates that the tendency, which is so pronounced in the Marattiaceae for forks and anastomoses within the major framework of the secondary walls of these cells to become associated with cell edges, does occur to some extent in the higher Filicales and is to an extent intermediate between the Marattiaceae and the higher Filicales in the Osmundaceae.

That there is a major framework within the secondary walls of these elements upon which a pattern of pits is superimposed is brought out by the following evidence: The secondary wall is often clearly thinner between adjacent horizontal pairs of pits than between vertical pairs of pits. In other words the pits can be seen to occur in valleys of the secondary wall. When the valleys are seen, they are seen not only on the faces, but also across the cell edges (Figs. 143, 144, 159, 162). These valleys are relatively easy to detect in *Blechnum*, *Pteridium*, *Cibotium*, and *Dicksonia*, as examples. The differences in thickness between the secondary wall between the valleys and that within the valleys is often great enough so that by focussing deeper into the cell the pits can be taken completely out of focus and the major structural framework of the cell only can be clearly seen.

The larger pits are always oriented parallel to the sides of the valley. The shorter ones, however, may have their axes somewhat tilted and even overlap within a given valley (Figs. 144, 159). One occasionally sees in a fern tracheid a close series of such short pits (Fig. 155) arranged in what might appear an alternate fashion; but in view of the observations presented above, they must be interpreted as being opposite.

The valleys, interpreted here as homologs of reticulate openings, may be oriented from transverse to vertical. Oblique orientation of valleys in association with walls which are too thick to clearly observe the valleys leads to a false impression of trans-edge alternate pitting in cells in which the pitting is actually trans-edge opposite. Extremes in departures from transverse orientation occur in *Dennstaedtia* (Fig. 145) and *Blechnum* (Figs. 142, 143, 146, 147) where obscalariform elements are common. Where elongate pits are oriented obliquely to vertically, the opposing pits in the adjacent cell are usually cross-matched (Fig. 285).

Additional evidence for the existence of major structural frame-work of the secondary wall upon which the pitted pattern is superimposed comes from the ontogeny of vessel members in *Pteridium*. Figures 157-159 represent portions of three different vessel members of successive stages in maturity from the last formed metaxylem of the *Pteridium*. Only a portion of a single vessel member is shown in each figure; the vertical lines represent the edges of the vessels or the walls of parenchyma cells the planes of which are at right angles to the plane of the drawing. In the young vessel member one can see a helical to reticulate system of thickening bands which show no regard for cell edges and cell faces (Figs. 157, 160). They appear at a stage when the vessel member has reached its maximum diameter and when the edges and faces are established and fixed. The wall between the thickenings is quite thin both on the faces and on the cell edges. In face view the thickening often shows some vertical lines due to differential staining within the band (Fig. 161). Wall deposition procedes along the wall radiating from the original thickenings and especially along the cell edges, so that pit-like openings are soon

evident (Fig. 158). This process is continued by the formation of more wall substance until the mature bordered pit is formed. The valleys between the pits, both on the faces and across the cell edges, are still clearly seen in the mature cell (Fig. 159). Membrane breakdown associated with perforation plate formation occurs at a stage in the development of the end wall comparable to that shown in Fig. 158, not Fig. 159, so that one cannot say that these pits associated with pore formation become larger, but it must be stated that they fail to reach their mature smaller size. The development of intervascular pitting in *Pteridium* follows the same sequence of events described above, the pitting, however, is more broadly scalariform (Fig. 162). The spiral thickening which appears first in the vessel members of *Pteriduum* can probably be referred accurately to " rims " or " bars " of Sanio.

Irregularities of the inner wall in the form of small projections, or vesturing, are common throughout many of the higher Filicales. These are illustrated for *Onoclea* in Fig. 156 which represents one pit enlarged from Fig. 155.

Throughout the higher Filicales small unlignified ridges at the base of the secondary thickening in the metaxylem elements are common. They may take the form of a single ridge in sectional view, similar to the one shown in Fig. 62, or a double one where each of the two surrounds the adjacent pit chamber, as shown for *Botrychium* in Fig. 100. In the Filicales they are never as pronounced as they are occasionally in *Botrychium*. These ridges may similarly be referred to as " Bars " of Sanio. Most of the earliest elements of the higher Filicales tend to have an unlignified primary wall with a more or less completely lignified secondary thickening.

Pit matching or pairing is variable in the metaxylem of certain higher Filicales. Pits in the faces of tracheary elements bordering parenchyma are more often without counterparts than paired. Some of the observations were made where the wall of the opposing parenchyma cell had enough thickness to avoid misinterpretation. Pairing in the intervascular pitting is also often not constant. It has already been mentioned above that pits which are oriented obliquely to vertically usually are cross-matched with pits in opposing walls. Even where the pits are transversely oriented in each of the opposing walls of adjacent elements, pairing may be irregular. In *Pteretis*, for example, one finds some ordinary pairing and in addition some scalariform pits which are matched with a vertical pair of pits in an adjacent cell. Sometimes this relationship is repeated regularly over a given face. A single elongate pit is often matched to a horizontal pair in an adjacent element, but this is a feature which occurs in most of the major groups of vascular plants.

There are numerous references to the structure of tracheary elements of the higher Filicales in existing literature. The late metaxylem scalariform element or scalariformly pitted element, as recent workers prefer to call it, has been generally ascribed to members of the group (Ogura, 1938; Atkinson, 1894; Bailey, 1925; Bower, 1923; Eames, 1936; Campbell, 1928; Prantl, 1875, 1881; Bliss, 1939; Boodle, 1901a, b; Ford, 1902; Gwynne-Vaughan, 1901; Link, 1841; Lange, 1891).

The spiral arrangement of pits and thus the trans-edge opposite arrangement was recognized by Link (1841), Bliss (1939), and Gwynne-Vaughan (1901). The latter two authors referred also to the way in which the fern tracheids split along a spiral line when treated with Potassium hydroxide as also did Russow (1872), which is referable to the overall framework of the cell walls.

The early xylem (proto- and early meta-) has similarly been described on a number of occasions, but descriptive terms were used without adequate illustrations so that it is rather difficult if not at times impossible to be certain of the way in which certain terms were used. Ambiguity in terminology is made clear in the table included in the discussion. Here it could be pointed out that " annular " has often been used to describe unstretched helical elements; " helical " has been used to describe unstretched annular elements and simple reticulate elements; " reticulate " more often has been used in the ferns to refer to early metaxylem elements and not to the simple reticulate elements

of the protoxylem (this is a guess); " scalariform " has been used to describe unstretched helical elements, simple reticulate elements, metaxylem reticulate elements with transverse openings, and also scalariformly pitted elements. The following descriptions are available: Ogura (1938) — the early xylem elements of ferns in general show ring- to spiral-form thickenings, later xylem is scalariformly pitted; Atkinson (1894) — in ferns generally there are spiral, reticulate, and scalariform tracheids; Bailey (1925) — " In the metaxylem of the Filicales, the scalariform reticulate thickenings frequently acquire overhanging margins and thus form transversely elongated pits . . . "; Bower (1923) — in ferns the tracheids of the protoxylem are spiral or reticulate as in most other vascular plants, scalariform tracheids in the metaxylem; Campbell (1928) — first elements are spiral or reticulate, later ones are large scalariform elements; Prantl (1875) — in Hymenophyllaceae, early xylem composed of reticulate elements, later ones scalariform; Prantl (1881) — the protoxylem is scalariform in *Schizaeae*, reticulate in other genera of *Schizaeaceae*, later elements in the family are scalariform; Boodle (1901) — in *Schizaeaceae*, the xylem elements are spiral, annular and scalariform; early xylem of the stem of *Lygodium* is finely scalariform; Boodle (1901b) — in *Gleichenia*, the early elements are annular and spiral, later ones scalariform; in some species all are scalariform; Chang (1927) — protoxylem elements of *Pteridium* are spiral; Demalsy (1953) — protoxylem elements of *Azolla* are spiral; Ford (1902) — protoxylem elements of *Ceratopteris* are spiral, later ones scalariform; Gwynne-Vaughan (1901) — protoxylem of *Loxsoma* composed of scalariform elements as is later formed xylem; Lange (1891) — elements of *Aspidium* are spiral, netted, and scalariform.

CYCADACEAE — In all the three genera of the Cycadaceae studied, the earliest elements were annular-helical hybrid types (Fig. 109). The helical portions tended to be mostly simple and single. An occasional fork and portion of a double helix could, however, rarely be found. The rings were simple or occasionally forked. A helical to reticulate series followed with reticulate elements appearing in the protoxylem, but not as early in terms of elongation of the organ as in the ferns. In other words they were only slightly stretched (Fig. 110). Some of the intermediate protoxylem elements possessed a secondary-secondary wall as in the Psilotaceae (Fig. 111). Later reticulate elements possess broad openings which traverse cell edges (Fig. 112) and grade into (in *Cycas*) a kind of pitted element with crowded pits which have broad angular borders and irregular although usually elongate and angular apertures (Fig. 113). This kind of pitted element preceded the scalariform element in the metaxylem of the stem of *Cycas*. The scalariform elements which can be found in the primary xylem of *Cycas*, *Dioon*, and *Ceratozamia* have pits with broad borders and wide apertures (Figs. 114, 115). The elongate pits of the metaxylem are oriented obliquely to transversely in the cell walls (Figs. 114, 115); they have never, however, been observed to approach vertical orientation. Pitting is primarily trans-edge opposite, this being difficult at times to determine due to oblique orientation of pits and rows of pits and also due to slight offsetting of adjacent pits in a row both on faces (Fig. 115) and across edges. Pit matching between protoxylem and metaxylem tracheary elements and parenchyma is often irregular (Fig. 116).

The following descriptions of early formed primary xylem elements of the Cycadaceae have appeared in the literature: Von Mohl (1832) mentions the occurrence of spiral elements and their modifications. Warburg (1883) describes scalariform cells which on stretching acquire the appearance of netted cells as the openings change from slit-like to more nearly rectangular. These are the protoxylem reticulate elements described above. Sifton (1915) described the primary ridges of cycad elements and referred to them as " bars of Sanio." Sifton (1920) characterized the protoxylem of cycads as spiral and scalariform and described the pitting in later formed elements in some detail. Penhallow (1907) described the early protoxylem as being

composed of spiral elements, and later ones of more compact structure with points of coalescence, and still later ones as scalariform, but still retaining more or less the lines of the original spiral. Bailey (1925) referred to cycad early formed xylem as scalariform reticulate, with later formed elements with more conspicuously bordered meshes which in still later formed elements break up into smaller bordered pits of opposite or alternate seriation. Chrysler (1937) refers to the presence in *Zamia* of scalariform reticulate elements in the protoxylem and scalariform elements in the later formed xylem, and in *Stangeria* of scalariform and spiral elements in the protoxylem.

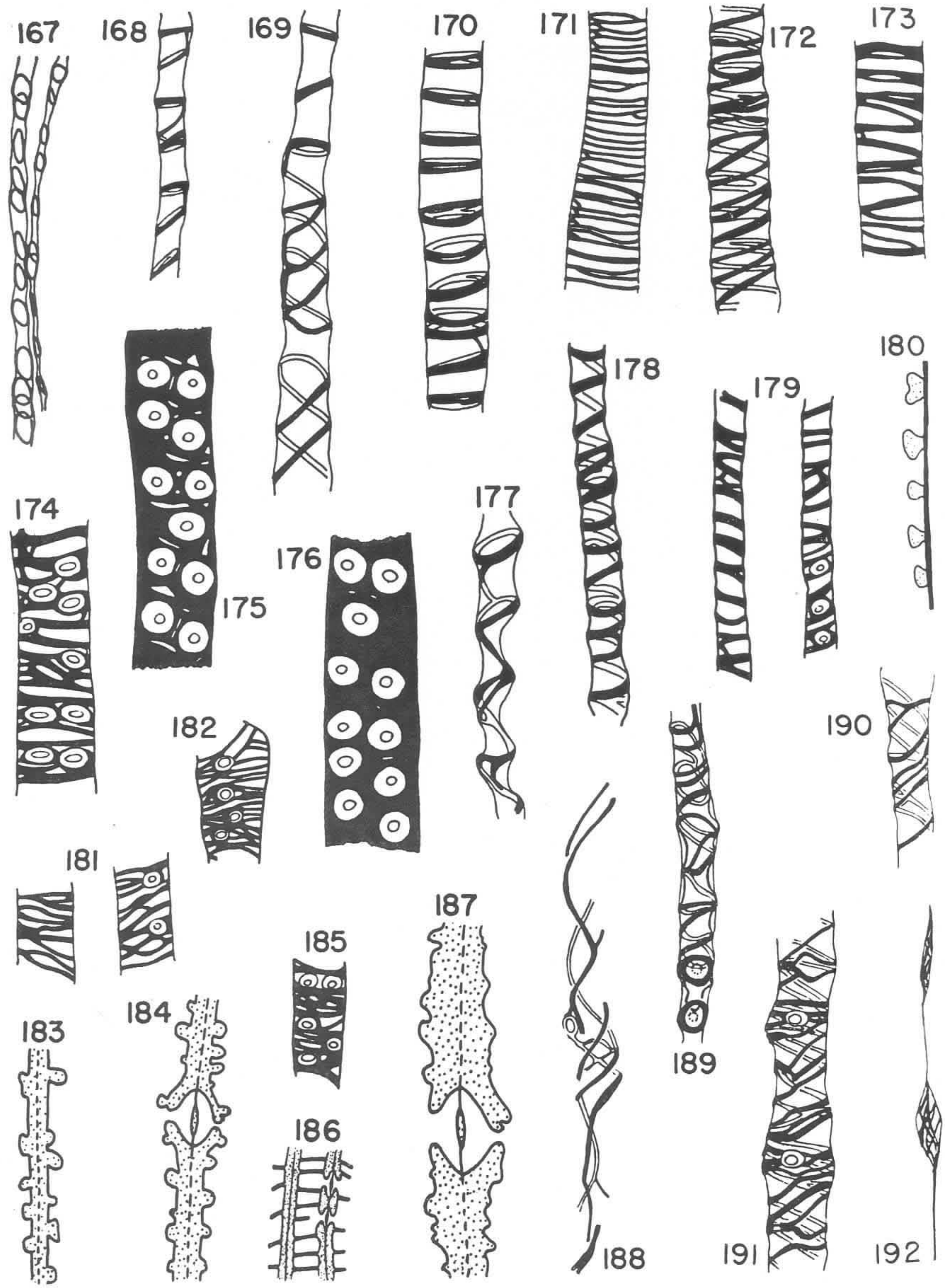
GINKGOACEAE — The earliest elements to mature in *Ginkgo* are very narrow annular elements (Fig. 167). The rings are simple, separate, lignified and rather thin. The primary wall is delicate and unlignified. These elements are followed in the ontogenetic sequence by slightly larger annular elements with thicker rings which are here and there interjoined by vertically or obliquely oriented strands of thickening (Fig. 168) or by elements of an annular-helical hybrid type (Fig. 169). The helical portions may be single or double (Fig. 169). Single helical portions may terminate with a ring (Fig. 169, third ring from the top). Double helical portions may also terminate with a ring or the two thickenings may fuse to a single one (Fig. 169) or the two thickenings may be terminated by a simple direct connection (Fig. 169, bottom). The latter feature seems to be especially uncommon in non-seed bearing vascular plants. Rings may be forked (Fig. 170) with the two lips of the double portion usually being close together.

The following elements in the sequence are helical (Figs. 171, 172). The helices have never been observed to be uniformly single, double or multiple. On the contrary, they show frequent points of branching so that the elements are singly-doubly (to multiple) helical (Fig. 172). When only one side of such an element (Fig. 171) is considered, it strongly suggests a reticulate element or a helical element with forks and anastomoses, but as far as could be determined, if the elements shown in Fig. 171 were to be stretched out completely, there would be no points of rupturing until the helix itself was straightened. There is often some degree of heterogeneity among the individual thickenings (Fig. 171). The transition of elements up to this point was seen much abbreviated in the short shoots and in the cotyledons.

The helical elements are followed by a helical to reticulate sequence. The early elements of the sequence suggest singly-doubly (to multiple) helices with frequent anastomoses (Fig. 173), the later ones being quite reticulate (Fig. 174). The first bordered pits appear in this sequence (Fig. 174).

Successively later formed elements show progressively smaller openings in the reticulum (Figs. 175, 176) until finally all suggestions of the reticulum are lost. It is suggested that the expression *tangential wall filling* be used to describe these events shown by the sequence of cell types. Similarly *centripetal wall filling* which can be detected in *Ginkgo*, especially in the cotyledons, is proposed to describe the sequence of changes from reticulate to pitted where the openings in the reticulum become progressively shallower, but not necessarily narrower as seen in face view, until the inner surface of the wall toward the end of the sequence is essentially smooth.

In discussing changes in the structure of tracheary elements it is necessary to distinguish among three kinds of changes. This may appear elementary and obvious to many readers, but a superficial examination of the literature quickly reveals frequent ambiguity. Firstly, there are *ontogenetic changes* which are undergone by individual cells during their existance. An example of such a change would be the change from helical or helical-reticulate to pitted of the vessel member of *Pteridium*. Secondly, there are *sequential changes*. These are the changes from one element to the next in an ontogenetic sequence of cell types, as for example the changes from helical through reticulate in several plant groups. Thirdly, there are *phylogenetic changes* which are interpretations that may be based in part on the other two types of changes as well as evidence from elsewhere.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FIGS. 167-192.

Bailey (1925) mentions the occurrence of circular bordered pits in early formed elements of *Ginkgo*, and also sporadic occurrence of elongate bordered pits. His interpretations resulting from these observations will be considered in a later section. Gunkel & Wetmore (1946) describe the early formed elements of *Ginkgo* as helical or rarely annular, with helical elements grading into circular bordered pitted types. They also mention the presence of bordered pits in early formed elements between the turns of the helical thickening.

TAXACEAE — The early elements in the ontogenetic sequence of *Taxus* are annular-helical hybrid types (Fig. 177). Forks in the helical thickenings occur commonly in the earliest elements resulting in rather short lengths of double helices (Fig. 177). Singly-doubly (rarely to multiple) helical elements follow (Fig. 178) with occasional anastomoses (Fig. 179). Bordered pits appear here in the sequence and are therefore earlier in the ontogenetic sequence than in *Ginkgo*. Heterogeneity among the thickenings can be detected, but it is not pronounced (Fig. 179). The primary wall of the early helical elements often tends to be appreciably thick (Fig. 180), but unlignified and is stretched to some extent.

Later helical elements show forks and some anastomoses, but the helical pattern remains evident. Figure 181 shows opposite sides of the same portion of an element from the stem of *Taxus*. If the two figures are mentally superimposed, the helical pattern becomes clear. Figure 182 shows a similar element from the axis of the female "strobilus". The elements shown in Figs. 181 and 182 were still part of the protoxylem as evidenced by the facts that they possessed unlignified primary walls and were found in incompletely elongated regions.

Later formed helical elements are similar in face view to those shown in Figs. 181 and 182. They illustrate *centripetal wall filling*, however, with an appreciable amount of secondary wall material over the entire inner surface of the cell, but considerably thicker in bands (Figs. 183, 184) giving to the surface view a pattern similar to the earlier elements of the sequence. *Tangential wall filling* is only slightly evident in *Taxus*. This can be seen if one compares Fig. 181 with Fig. 185 which is a reticulate element in the late metaxylem. Figure 187 shows a further stage in *centripetal wall filling* and is a sectional view of the wall of the same cell shown in Fig. 185. *Centripetal wall filling* is not complete in *Taxus*, but toward the end of the metaxylem sequence and into the secondary xylem the tracheids show the so-called "tertiary" thickening (Fig. 186).

CONIFERALES — The ordinal name Coniferales as used here excludes the Taxads, following the opinion of Florin (1951). The variation from family to family within the Coniferales is not appreciable. The differences between the Taxaceae and the Coniferales are not very great as will be appreciated, but among the conifers the difference from family to family is of an even lesser order of magnitude. For this reason, only the elements of *Pinus* are illustrated and described in detail.

The earliest protoxylem elements of *Pinus* are helical (Figs. 188-191) with thin unlignified primary walls. The helices are never diagrammatically simple and rarely single. They show frequent forks

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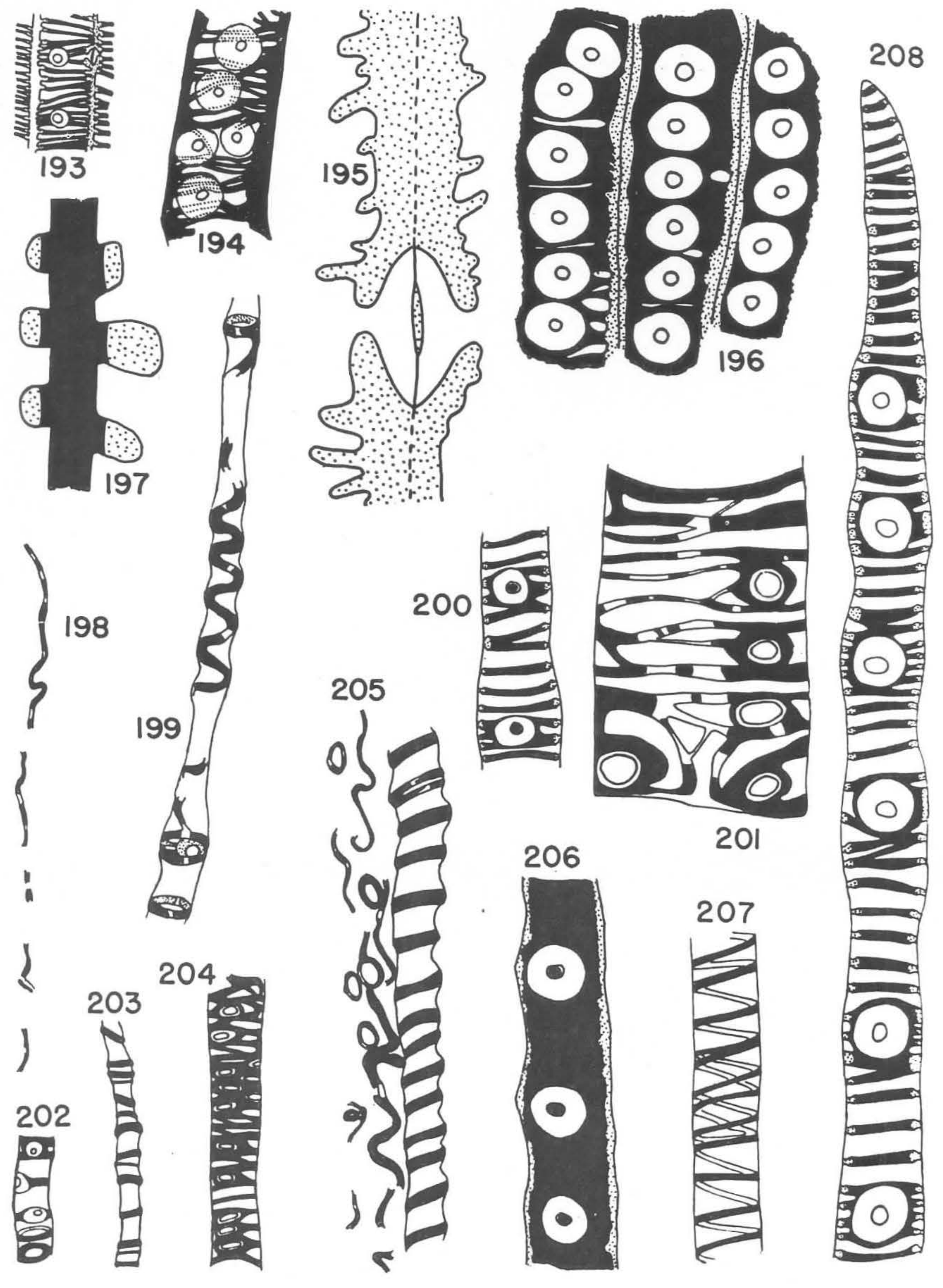
FIGS. 167-192 — Figs. 167-176. Portions of tracheary elements from the long shoot (2-year old seedling) of *Ginkgo biloba*. × 666. Figs. 177-179. Portions of tracheary elements from the stem of *Taxus baccata* (*sens. lat.*). Fig. 179 shows views of opposite sides of the same cell. × 666. Fig. 180. Sectional view of the wall of the same cell shown in Fig. 179. × 1660. Fig. 181. Views of opposite sides of the same tracheid from the stem of *T. baccata*. × 666. Fig. 182. Portion of a tracheid from the axis of the female "strobilus" of *T. baccata*. × 666. Figs. 183, 184. Sectional views of walls of late helicoid elements from the stem of *T. baccata*. × 1660. Figs. 185, 186. Portions of tracheids from the stem of *T. baccata*. × 666. Fig. 187. Sectional view of the wall of the cell shown in Fig. 185 and opposing wall of the adjacent cell. × 1660. In Figs. 180, 183, 184, and 187, stippled areas are lignified, blackened areas are unlignified. Figs. 188-192. Portions of tracheary elements of *Pinus mugho*. × 666. Figs. 188, 189, 191, 192 from a young long shoot; Fig. 190 from the female cone axis.



FIGS. 193-208.

and therefore vary in their degree of multiplicity (Figs. 188, 190, 191). Some of the relatively early (but not earliest) elements show extra irregularly disposed interconnections and therefore tend somewhat to be reticulate. The multiple helical elements or multiple helical with a somewhat reticulate tendency on complete stretching (Fig. 192) tend to leave close bunches of wall thickenings here and there separated by completely flattened portions of the cell through which one to several strands are continuous. Suggestions of annular thickenings are rare in *Pinus*.

The circular bordered pit appears in the protoxylem elements of *Pinus* (Figs. 188, 189, 191) at a stage in the ontogenetic sequence somewhat earlier than in *Taxus*, but among the other Coniferales there is some variation in this respect. Among the conifers, however, they seem never to appear in the sequence as late as they do in *Ginkgo*.

As in *Taxus*, the late helical members of the ontogenetic sequence show pronounced *Centripetal wall filling* (Figs. 195, 197). The base wall on the inner surface of which is superimposed the helical pattern may occasionally be unlignified even well into the helical thickenings (Fig. 197). In most other conifers, the entire base wall as well as the helical thickenings is usually entirely lignified. In *Pinus*, well into the metaxylem, the entire wall is similarly lignified (Fig. 195).

The helical pattern becomes lost or obscure as *centripetal wall filling* progresses in the ontogenetic sequence (Fig. 194).

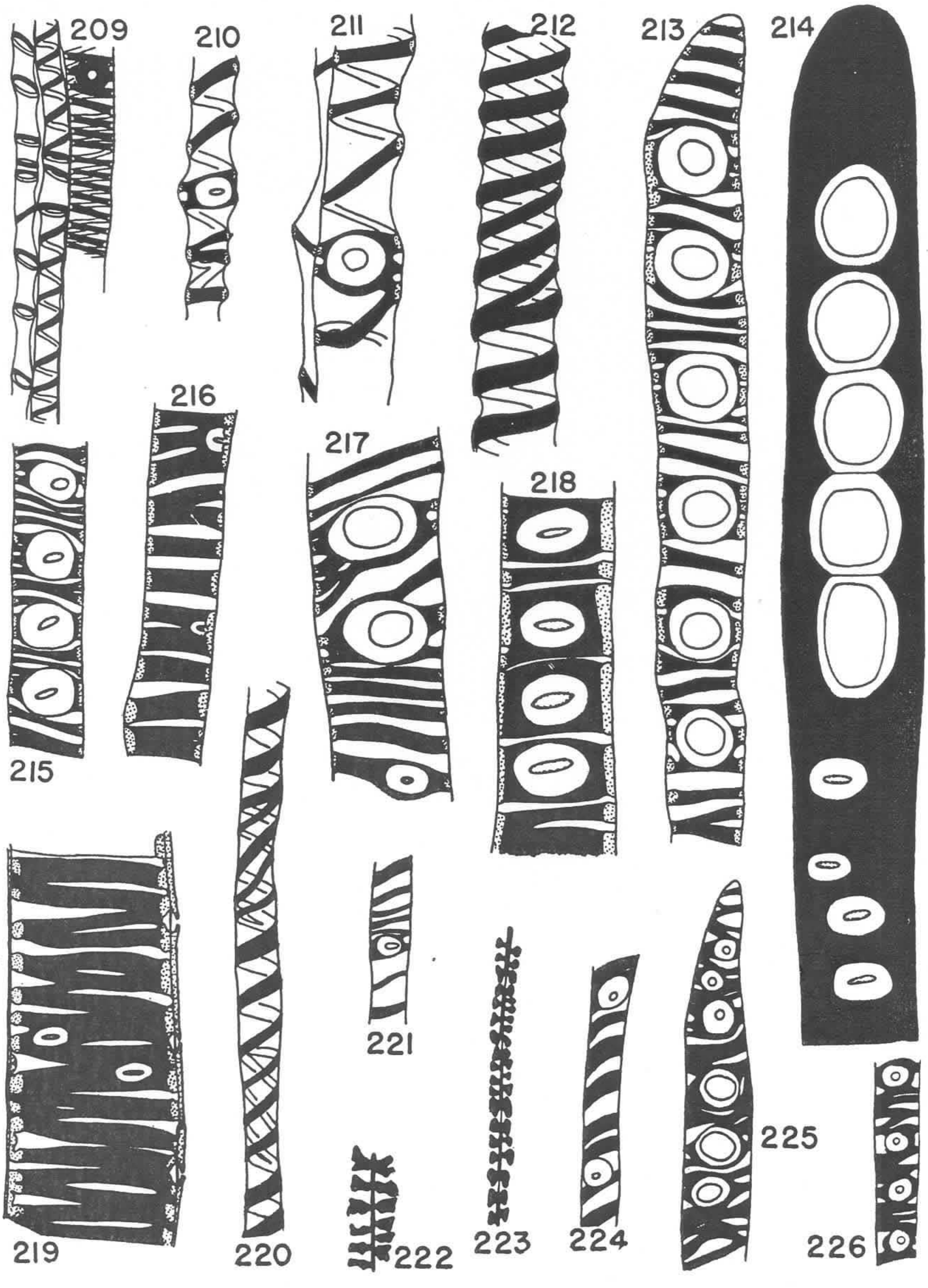
In addition to *centripetal wall filling*, *tangential wall filling* is expressed in *Pinus* as well as in most other conifers. This is illustrated in Fig. 196.

The early formed tracheary elements of conifers are referred to in several previous publications. Penhallow (1907) states that spiral tracheids are typical of the protoxylem of all genera showing a more or less definite tendency of the spirals to coalesce here and there. Thompson (1914) describes the primary xylem of *Araucaria* as containing "ringed, spiral, and scalariform" elements as well as "transitional scalariform" elements which he described as scalariform elements which show signs of becoming typical multiseriate bordered pitted. Pool (1929) refers to *Araucaria* as having spiral tracheids with one, two or less frequently three spiral thickenings and thin primary walls which become irregularly stretched in the protoxylem and tracheids with 3 to 6 close spiral thickenings and thin primary walls in the metaxylem. Crafts (1943) describes *Sequoia* as having tracheids with single spirals in the early formed xylem and double or more complex spirals in the later formed xylem. Jeffrey (1912) speaks of scalariform elements in the protoxylem of *Araucaria*.

The presence of circular bordered pits in the early wood of conifers was described by Bailey (1925), but was illustrated earlier by Hartig (1878) and Jeffrey (1917). Later, Crafts (1943) refers to them in *Sequoia*, Buchholz (1933) in *Cedrus*, and Pool (1929) in *Araucaria*.

EPHEDRACEAE — The earliest elements of *Ephedra* have thin unlignified primary walls internal to which is a series of diagrammatically simple rings with, in some cases, an occasional interconnecting gyre (Fig. 205). Succeeding elements are less annular and more helical (Fig. 205) and still later ones are entirely helical.

FIGS. 193-208 — Figs. 193-197. *Pinus mugho*. Figs. 193, 194. Portions of tracheary elements from the long shoot within the region of elongation and from the female cone axis respectively. × 666. Fig. 195. Sectional views of the walls common to two tracheids from the metaxylem of the female cone axis. These elements were reticulate in appearance in surface view. × 2330. Fig. 196. Portions of three successive elements from the metaxylem of the female cone axis. The earliest element is to the left, the latest to the right. × 666. Fig. 197. Sectional view of the wall of the element shown in Fig. 193. × 2330. In Figs. 195 and 197, blackened areas are unlignified, stippled areas are lignified. Figs. 198-201, 204-208. Portions of tracheary elements from the stem (198-200, 204-208) and leaf (201) of *Ephedra* sp. In Fig. 198, 199, and 201, blackened areas are lignified, clear areas within the thickenings are unlignified. Blackened areas within pits in Figs. 200 and 206 represent tori. Figs. 198-200, 204-208. × 666. Figs. 201, × 1670. Figs. 202, 203. Portions of tracheary elements from the female strobilus of *Ephedra foliata*. × 666.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FIGS. 209-226.

elements which possess a single, simple helix are common. Diagrammatic representations of the singly-doubly helical element may also be found (Fig. 207). Heterogeneity among the thickenings of the early elements is usually not pronounced, but this feature was found well expressed in the axis of the female strobilus of *E. foliata* (Fig. 203). Bordered pits appear in the early protoxylem elements (Figs. 199, 202) and in succeeding elements (Figs. 200, 201, 204, 206).

Later helical elements become progressively more reticulate in the sequence. There are generally a considerable number of forks and anastomoses associated with the pit trusses (Fig. 200) or pore trusses (Fig. 208) and if the pits are close together vertically, the element is more reticulate than helical. Reticulate elements such as the one illustrated in Fig. 204 are not common in the stem and their transition from clearly recognizable helical elements tends to be rather abrupt. In the leaf, on the other hand, reticulate elements are common (Fig. 201).

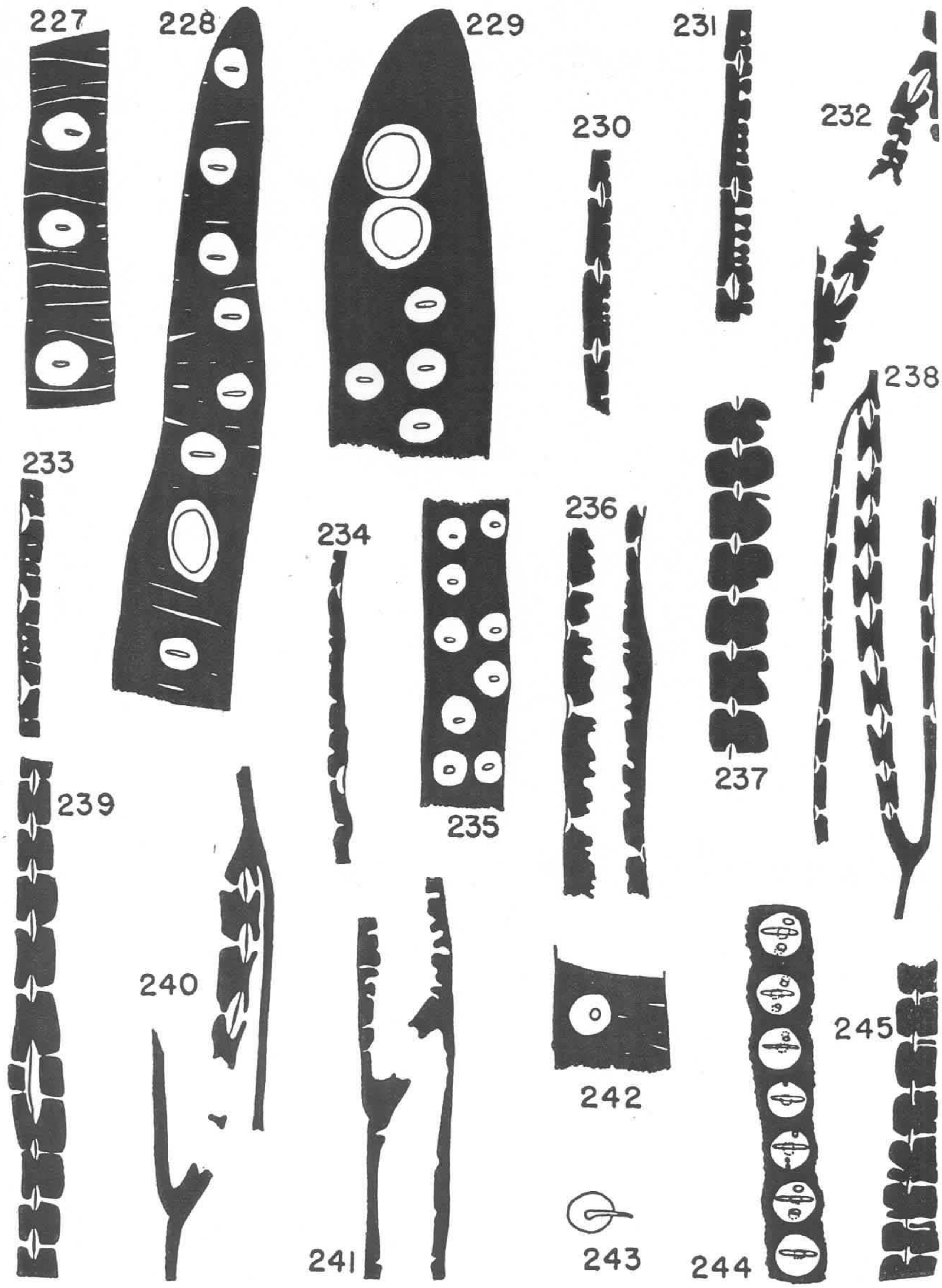
Centripetal wall filling can be seen toward the end of the sequence of cell types in the metaxylem (Fig. 206). *Tangential wall filling* in the sequencial sense occurs.

Certain of the larger pits in the helical and later elements lose their pit closing membranes and become pores (Fig. 208) as is well known (*see* Bailey, 1944). In *Ephedra* the pores tend to develop in uniseriate longitudinal series in the protoxylem, but uniseriate arrangement is usually lost in the late metaxylem and into the secondary xylem where the pores tend to be in compact groups. The simple perforation is thought not to exist in *Ephedra*, but one was observed in the secondary xylem. The perforation plate was actually simple on one side only, and was matched with a group of four pores in the opposing wall of the next vessel member in the vertical series.

The primary wall of tracheary elements of *Ephedra* tends to be unlignified throughout the primary xylem and the secondary wall for the most part lignified. Occasionally, however, one will see in a face view of an element unlignified areas in the secondary system (Figs. 198, 199, 201, 205, clear areas). These were seen occasionally in *E. antisyphilitica* and commonly in *E.* sp. On stretching of the early protoxylem elements, the thickenings often rupture across these unlignified areas (Figs. 198, 199, 205). The unlignified areas could be seen in protoxylem elements rather close to the shoot tip and therefore seem to represent areas where lignin was never added to the cellulose framework rather than areas where lignin had been digested away later.

GNETACEAE — Simple annular elements appear first in the protoxylem sequence of *Gnetum* (Fig. 209). These are followed by annular-helical hybrid types of elements and then by helical elements. The helical elements are single, double or singly-doubly (Figs. 209-212). The primary wall of the early elements of *Gnetum* is thin and unlignified. This characteristic is usually present throughout the primary xylem and into the secondary xylem. An unusual exception to this generalization is shown in Fig. 219 which shows a slightly thickened and lignified base wall. Bordered pits appear relatively early in the protoxylem (Fig. 209) and are present in all subsequent elements in the sequence (Figs. 209-212, 214, 215-219). The pits are generally vestured as the result of the presence of small outgrowths around the pit apertures (Figs. 210, 214, 215, 218). The pit truss in the early elements (Fig. 209) tends to be a group of secondary thickenings, but in

FIGS. 209-226 — Figs. 209-218. Portions of tracheary elements from the stem of *Gnetum gnemon.* Structures in Figs. 209, 210, 215, 216, and 218 are bordered pits while the one in Fig. 211, those in Fig. 213, the five larger ones in Fig. 214, and the two larger ones in Fig. 217 are pores. Fig. 219. Portion of a tracheary element from the stem of *Gnetum leyboldii*. Figs. 220-226. Portions of tracheary elements from the axis of the female strobilus of *Welwitschia*. Sectional views of double walls in Figs. 222, 223. Note the four pits in Fig. 223. The structures in Figs. 221, 224, and 226 are pits, while in Fig. 225 the three upper ones are pits and the three lower (larger) ones are pores. All × 666.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FIGS. 227-245.

later elements the number of secondary thickenings supporting the bordered pit become reduced progressively until in the later protoxylem and early metaxylem the secondary wall around the pits is in the form of a sheet (Fig. 218). In other words, tangential wall filling takes place in the vicinity of the pits more than elsewhere. Eventually, toward the end of the metaxylem, tangential wall filling is complete (Fig. 214). The helical pattern often seems to be preserved in the sequence of cell types until the wall is almost completely tangentially filled. Only occasionally does one see what can be clearly referred to as a reticulate element (Fig. 219).

As in *Ephedra*, certain pits are larger and lose their pit closing membranes to become pores (Figs. 211, 213, 214, 217). In the protoxylem the pores are in uniseriate order near the ends of the cells (Fig. 213) as in *Ephedra*. In the metaxylem the pores are larger and are in closer proximity to each other (Fig. 214).

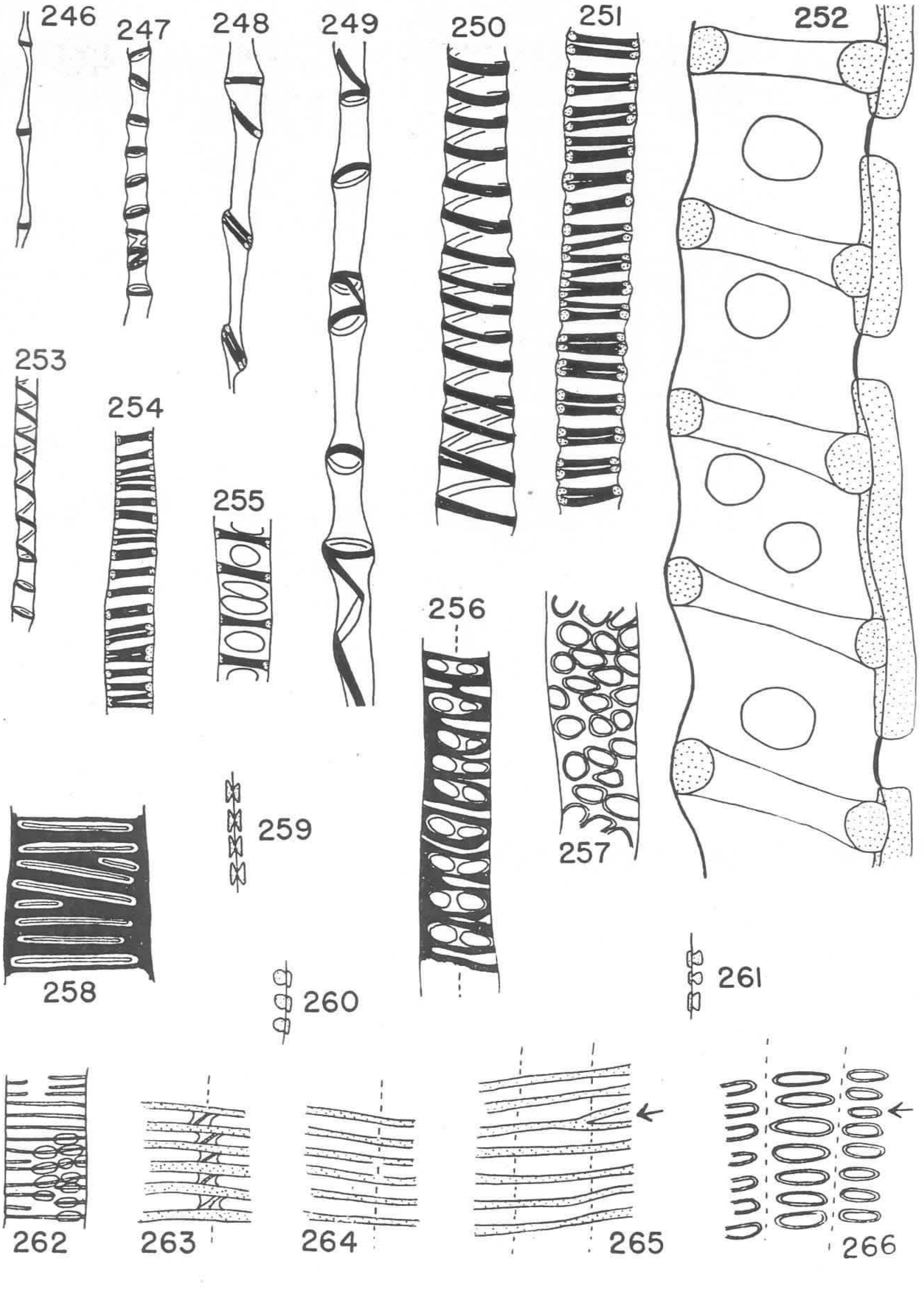
WELWITSCHIACEAE — The early protoxylem elements of *Welwitschia* are either singly helical or singly-doubly helical (Figs. 220, 224). The base wall (presumed primary walls in the early elements) tends to be slightly thickened in the early elements of the sequence and more and more thickened in the later elements (Figs. 222, 223). In sections of mature organs (stems, roots, inflorescence axes, and strobilar axes) all of the cell wall layers are usually seen to be strongly lignified. Sectional views of the helical thickenings show unusual and irregular shapes (Figs. 222, 223).

Bordered pits which are often vestured as in *Gnetum* appear in the relatively early protoxylem and in subsequent elements (Figs. 221, 224-229). Some of these structures develop into pores as in *Ephedra* and *Gnetum*. In the early elements of *Welwitschia* rows of pores are uncommon. The single pore is by far of the most common occurrence (Figs. 228, 232, 241), two pores at the same end of an element are less frequent (Figs. 229, 240), and three pores have been seen only once (Fig. 225). Only singly occurring pores have been seen in last formed metaxylem and "secondary" xylem. Previous reports indicate that only the single pore exists in *Welwitschia*.

The helical pattern of the protoxylem gives way in the sequence to a reticulate one as numerous forks and anastomoses appear (Figs. 225-228). In addition, the openings of the reticulum become narrower and narrower as the result of well expressed tangential wall filling (Figs. 226-229).

Centripetal wall filling is similarly well expressed in *Welwitschia*. The base wall, which is a presumed primary wall in the earliest members of the sequence, is seen to be progressively thicker in later and later formed elements and therefore the more internal thickenings, which are

FIGS. 227-245 — *Welwitschia*. Figs. 227-229, 235, 242. Portions of face views of tracheary elements. In Fig. 228, one pore is shown; in Fig. 229, two pores are shown. Fig. 230. Sectional view of the walls of two adjacent tracheary elements. The cell to the left is a pitted element; the one to the right is a reticulate element. Fig. 231. Same as Fig. 230, but different cells. Fig. 232. Sectional view of the end walls of two reticulate vessel elements in a series. One pore is shown. Fig. 233. Sectional view of the wall of a tracheary element. None of the indentations or grooves in the walls here are lateral extensions of elongate inner pit apertures. Fig. 234. Same as Fig. 233, but essentially all of the indentations or grooves here are the lateral extensions of elongate inner pit apertures. Fig. 236. Sectional view of the same cell in Fig. 235. Fig. 237. Sectional view of the adjacent walls of two pitted elements. Fig. 238. Sectional view of the ends of two overlapping pitted elements. Fig. 239. Sectional view of the adjacent walls of two pitted elements showing a pit pair with several apertures. Fig. 240. Sectional view of the end walls of two vessel elements in a series. Two pores and three pits are shown. Fig. 241. Same as Fig. 240, but reticulate elements and one pore shown. Fig. 243. The same pit shown in Fig. 242, but at a lower focal plane, showing that the slit-like opening to the right of the pit in Fig. 242 is in reality the edge of the inner pit aperture. Fig. 244. Bordered pits with multiple apertures in face view. Inner apertures shown by solid lines, outter apertures by dotted lines. Fig. 245. Sectional view of the wall of the same cell shown in Fig. 244 and the opposing wall. Figs. 227-243 from the major axis of the male inflorescence. Figs. 244, 245 from the root. All × 666.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FIGS. 246-266.

helical in the earlier members of the sequence and reticulate in the later ones, become relatively less and less pronounced until the inner surface of the cell is essentially smooth. The entire sequence with respect to centripetal wall filling is shown by Figs. 222, 223, 230 (right side), 231 (right side), 232, 233, 241, 236, and 238. The walls of the tracheary elements of *Welwitschia* are often so thick and densely staining that irregularities on the inner wall are not seen in surface view unless they are of considerable magnitude, e.g. Fig. 235 is a representation of the surface view of the same element shown in sectional view in Fig. 236.

The inner pit apertures of late formed tracheary elements of *Welwitschia* are very narrow and elongate, and oriented nearly transversely to the axis of the cell. The elongate inner aperture is often not situated symmetrically, but may extend for a greater distance toward one side or another. The inner apertures at a given focal plane may occasionally appear in face view to be a part of the cell's inner reticulum, e.g. the slit to the right of the pit in Fig. 242 at another focal plane appeared as in Fig. 243. In sectional view the edges of elongate inner apertures if viewed at a focal plane which does not include the pit chamber will appear to be irregularities on the inner surface of the wall. As far as could be determined, all of the apparent irregularities on the inner surface of the wall shown in Fig. 234 and some of those in Fig. 236 are the edges of elongate inner pit apertures.

Pits in *Welwitschia* often show multiple apertures. In the series of pits shown in Fig. 244 in face view and in a similar series from another part of the same cell in Fig. 245 in sectional view, multiple apertures are shown. In Fig. 244, inner apertures are shown with solid lines while outer apertures are shown with dotted lines. In each of these pits, there is one major pit canal and one to several minor ones. The pit pair shown in Fig. 239 (fourth from the bottom) had two major pit canals in either member of the pair.

The early elements of the three "Gnetalean" genera are referred to rather briefly in previous literature. Pearson (1929) describes *Ephedra* as having "normal gymnospermous structure, *Gnetum* as having elements with spiral, annular and reticulate thickenings among which bordered pits occur at intervals and *Welwitschia* as having annular, spiral and reticulate elements and in addition elements in which all three kinds of thickening are combined. Bailey (1925) described the occurrence of circular bordered pits in early formed elements of *Ephedra*.

The simple perforation plates which occur commonly in *Gnetum* and *Welwitschia* and which have been seen only once in *Ephedra* have been interpreted (Bailey, 1944) as being derived by the "fusion" of several smaller ones. The evidence in support of this interpretation comes primarily from *Gnetum*, where in the primary xylem perforation plates are at first composed of a linear series of pores,

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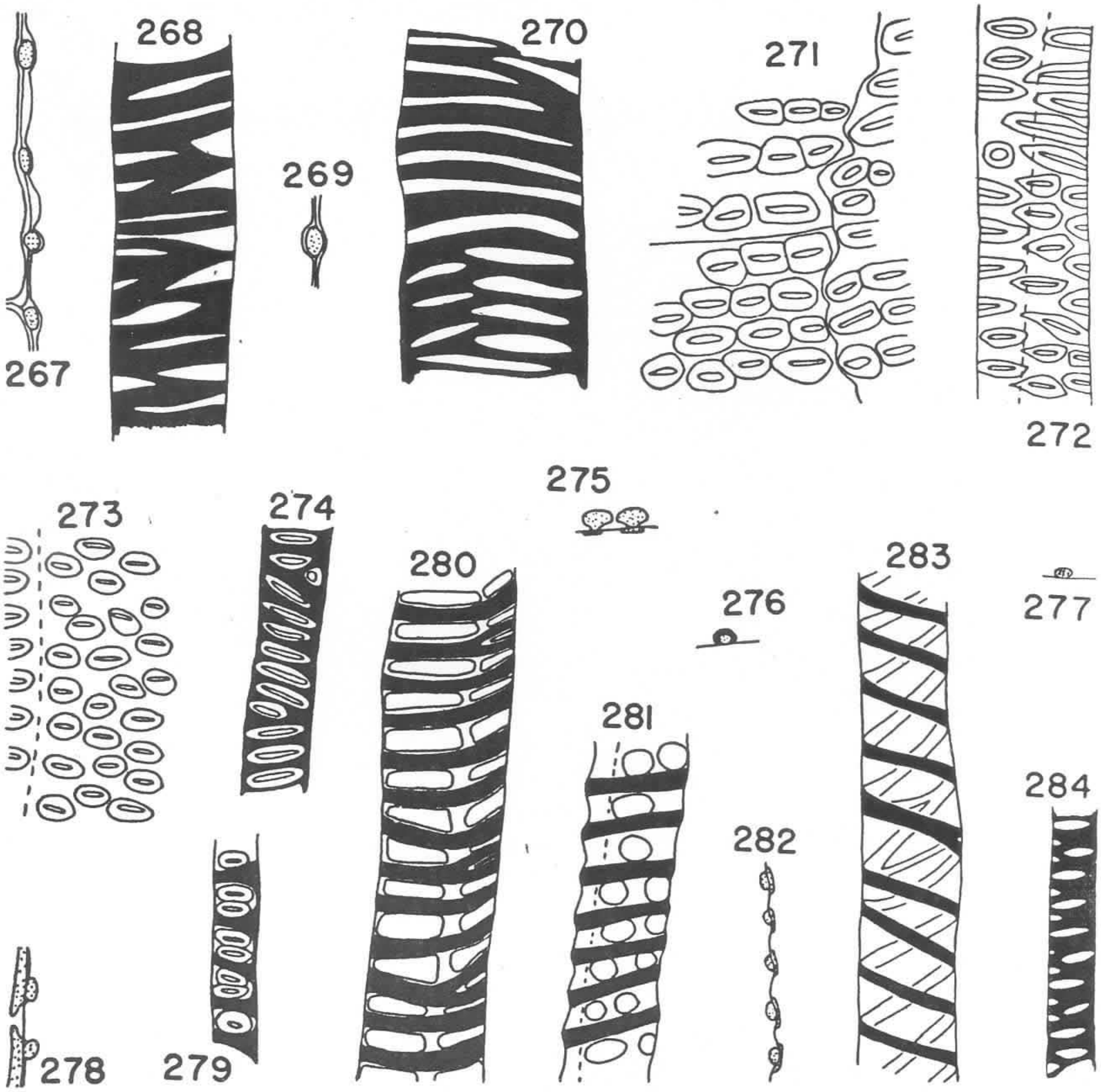
FIGS. 246-266 — Figs. 246-251. Portions of tracheary elements from the stem of *Hedera helix*. × 666. Fig. 252. Portion of a protoxylem element and wall of an adjacent parenchyma cell from the stem of *Michelia fuscata*. × 4440. Figs. 253-257. Portions of tracheary elements from the stem of *Ligustrum vulgare*. × 666. Fig. 258. Portion of a metaxylem element from the stem of *Liriodendron tulipifera*. × 666. Fig. 259. Sectional view of the walls of two adjacent metaxylem elements from the stem of *Magnolia grandiflora*. × 666. Fig. 260. Sectional view of the wall of the same cell shown in Figs. 263 and 264 and the wall of the adjacent parenchyma cell (on right). × 666. Fig. 261. Sectional view of the wall of the same cell shown in Figs. 265 and 266 and the wall of an adjacent parenchyma cell (on left). × 666. Fig. 262. Face view of a portion of a metaxylem element from the stem of *Casuarina equisetifolia* and the outlines of the simple pit pairs shared with overlying parenchyma. Only the slit-like apertures of the tracheary element are shown, the borders which are very broad are omitted for simplicity. × 666. Fig. 263. Outter focal plane of the face view of an early metaxylem element from the stem of *Magnolia grandiflora*. × 666. Fig. 264. Inner focal plane of the same portion of the same cell shown in Fig. 263. × 663. Fig. 265. Inner focal plane of the face view of a metaxylem element from the stem of *Magnolia grandiflora*. × 666. Fig. 266. Outer focal plane of the same portion of the same cell showh in Fig. 265. Arrows indicate points of correspondence.



FIGS. 267-284 — Figs. 267-271. From the stem of *Citrullus vulgaris*. Fig. 267. Sectional view of the wall of a helical element (right) and the opposing walls of parenchyma (left). Stippled wall is lignified, clear wall is unlignified. Fig. 268. Portion of a tracheary element. Fig. 269. Sectional view of the wall of the same cell shown in Fig. 270, and the wall of an adjacent parenchyma cell (on right). Lignified wall is stippled. Fig. 270. Portion of a tracheary element. Fig. 271. Portion of a pitted element showing (sinuous line) an edge of the vessel element which corresponds to the intersection of the parenchyma cell walls, the plane of which is at right angles to that of the drawing. Figs. 272, 273. Portions of tracheary elements from the stem of *Hisbiscus esculentus*. Broken line indicates a cell edge. Figs. 274-284. From the stem of *Cordyline* sp. Fig. 274. Portion of a metaxylem element. Fig. 275. Sectional view of the wall of a metaxylem element (top) and the opposing wall of a parenchyma cell (bottom). Fig. 276. Sectional view of a part of the wall of a helical element. Fig. 277. Sectional view of a portion of the wall of a reticulate element. Fig. 278. Sectional view of the wall of a pitted element (left) and a helical element (right) showing a half-bordered pit pair. Fig. 279. Face view of the same double wall shown in Fig. 278. Figs. 280, 281. Portions of protoxylem elements. Broken line represents a cell edge. Fig. 282. Sectional view of the wall of a helical element (left) and the opposing wall of a parenchyma cell (right). Figs. 283, 284. Portions of tracheary elements. All × 666.

then a transition to grouped pores which are closer and closer in proximity to each other, then grouped pores showing various stages of "fusion" which persist along with the large simple perforation well into the secondary xylem. A similar sequence

rarely showing complete fusion is to be found in *Ephedra*. The "fusion" interpretation is therefore well supported in *Gnetum* and in *Ephedra*. In *Welwitschia*, however, one finds in the early primary xylem mostly vessel members with relatively large simple perforations, occasional vessel members with two pores, and rarely with three. No evidence of fusion of adjacent pores has been found, and where the pores are in twos or threes, they are always linearly arranged. The hypothesis that a number of smaller pores phylogenetically fused to form a larger one seems quite unsupported in *Welwitschia*, but rather it is suggested that there has been a reduction in the number of pores and, therefore, the single pore which is usually to be found on the end plate of the vessel member of *Welwitschia* more likely is the homolog of one of the individual pores of the Ephedroid type of multiple perforation plate and represents a phylogenetically transformed single bordered pit.

ANGIOSPERMS — The size of the sample of flowering plants used in this study permits few generalizations as to their primary tracheary element structure. This is similarly true even if this sample is added to all those which have been previously described. From the point of view of the present study, the mere presence of certain structural features is of some importance. Little or nothing can be said with certainty concerning the absence of certain features in the angiosperms as a whole, obviously.

In terms of the very little information presently at hand, the angiosperms may possess the simplest and most diagrammatic structural types of early protoxylem elements. The simplest type of protoxylem element to conceive is the one in which there is a thin primary wall and no secondary wall as has been described from the embryo of *Gleditsia* (List, 1958) where it exists only for a very short time. This type of protoxylem element may be of more widespread occurrence, but to date has not been observed elsewhere. The simple annular element with distinct, unelaborated rings is probably widespread among angiosperms (Figs. 246, 247). It has been described and illustrated in essentially every textbook of General Botany and Plant Anatomy published in the past 150 years. It was not well known until the work of Von Mohl (1839).

Some variations do occur among the annular elements of the angiosperms. The full extent of the range in variation will be known only after a very careful study of many hundreds of angiosperms. Forked rings, or directly attached rings, occur apparently sporadically. It is not known whether or not there are any angiosperms which possess extensive series of forked rings. Pairs of rings with simple indirect connections similarly occur; these are illustrated in Figs. 247 and 249 from *Hedera*. Rings in which there is an internal groove have been seen in *Hedera* (Fig. 248). Here and there the groove is deep enough to produce some doubling. Annular-helical hybrid types of elements are of course well known (Figs. 253, 249).

The simple helical elements have been known in angiosperms since the observations of Grew (1682) and Malpighi (1675) and have been illustrated and described many times. The double helical elements are similarly well known. The apparently multiple helical elements mentioned by de Bary (1877) and Skutch (1927) as occurring in *Musa* and probably also those described by Treviranus (1806) from *Amomium* with occasionally more than a dozen parallel helical thickenings are not of a simple structure. Adjacent thickenings in the groups of parallel ones are interconnected by fine strands of secondary wall material. This has also been observed in *Pandanus*.

The helix may be internally grooved as another variation. This was illustrated by Brisseau-Mirbel (1815) and Esau (1953). The groove occasionally is deep enough here and there to result in doubleness of the thickening (Figs. 250, 251, 254).

Branched helical thickenings are apparently not uncommon among angiosperms (Figs. 250, 283). The singly-doubly (to multiple) type of helical element so diagrammatically represented in *Ephedra*, *Gnetum*, and *Welwitschia* has not been observed.

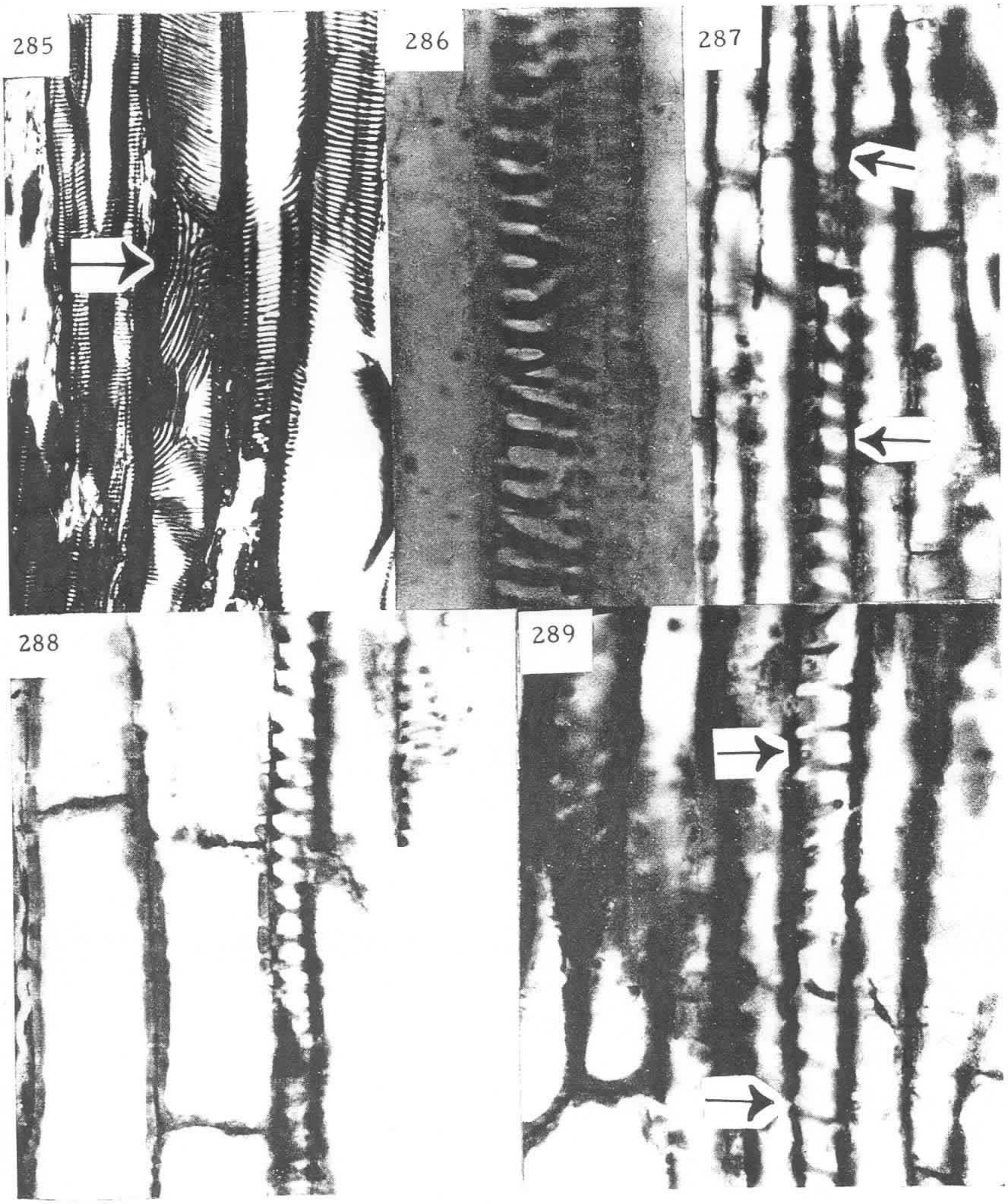
The reticulate element shows considerable variation among angiosperms. A

survey of various angiosperm groups in terms of details of structure of the reticulate elements found in the primary xylem should prove quite rewarding. Among dicots, reticulate elements in which the openings in the reticulum are transversely oriented and cross cell edges are common (Figs. 268, 270) [*see* also Esau (1953), Fig. 11.4; Eames & McDaniels (1947), Fig. 62; Jeffrey (1917), Fig. 13]. These elements often follow in the sequence of cells in the primary xylem other elements which are intermediate between helical and reticulate in that they possess obvious helical organization, but in addition anastomoses between adjacent gyres. Reticulate elements in which the openings are more or less of circular form but with slight borders (Fig. 257) occur; the extent to which this type of element occurs among angiosperms is not known. Irregular reticulate elements in which the openings are circular to elongate to irregular and oriented from transversely to vertically all within the same cell are known. See the illustrations of Cheadle (1943) Fig. 8 and Esau (1953) Fig. 11.5. A survey of angiosperm primary xylem may show the irregular reticulate element to be more or less characteristic of certain monocot families. In certain monocots, e.g. *Zebrina, Cyperus*, a type of reticulate element occurs in which the openings are large, rectangular, and somewhat elongate transversely, and are uniformly trans-edge opposite. It is possible that a survey will show that this type of reticulate element also is of restricted distribution. Occasionally openings in reticulate elements develop rather extensive borders (Fig. 272). Note that this element from the stem of *Hibiscus* shows openings crossing cell edges.

Angiosperm pitted elements have been described in possibly hundreds of publications. It is desirable to point out several features of the elements of certain genera here in order to arrive at a generalized concept. Pitted elements, either transitionally pitted or circular pitted, generally show some rowed arrangement on the faces. The rows may be either transverse or slanted (Figs. 271, 273). The rows are often disturbed suggesting a branching of the structural organization of the wall (Fig. 271). This is considered comparable to those points where, in the scalariformly pitted elements, a given elongate pit ends within a face and is not situated opposite another (Figs. 258, 274). The pits, in addition, in those few angiosperms in which this characteristic has been observed, are trans-edge opposite (Figs. 273, 271), that is, the rows may be seen to continue on adjacent faces.

The primary cell wall in angiospermous primary xylem tracheary elements is often thin and unlignified (Fig. 277) as is stated in essentially every textbook of plant anatomy. It may also be to a large extent lignified as in many of the elements of *Cordyline*, or the secondary wall may show a lignified core and an unlignified inner portion (Fig. 276).

A secondary-secondary cell wall of the type observed in the Psilotaceae and in the Cycadaceae is quite pronounced in certain Angiosperms. It has been seen in *Magnolia, Liriodendron, Michelia, Citrullus*, and *Cordyline*. In the three Magnoliaceous genera it was most distinct. It was present only between the secondary thickenings (Figs. 252, 278, 279) in all, but *Citrullus* where it also covered the secondary thickenings (Figs. 267, 269). Pits were frequently found in the opposing walls of elements adjacent to early primary xylem elements. Figure 252 (*see* also Figs. 287-289) shows such pits in face view and also in sectional view where it can be seen that the secondary-secondary wall of the helical element outlined the matching pits to those in the adjacent parenchyma cells. The pits seen in face view in Figs. 255, 256, 280 and 281 and in sectional view in Figs. 275 and 282 may be unmatched pits in that the walls of the tracheary elements were so thin that the counterpart pits could not be detected. It will be noted that the simple pits in the parenchymatous elements (lower side in Fig. 275, and right side in Fig. 282) are in these cases smaller in diameter than the width of the " border " on the opposite side. Pits observed between the secondary thickenings of primary xylem elements were never seen to cross cell edges. Figure 262 illustrates a condition from the metaxylem of *Casuarina* comparable to those described above. Here is shown a face view of a



FIGS. 285-289. Fig. 285. Metaxylem elements from the stem of *Dennstaedtia*. Arrow indicates crossing elongate pits. × 100. Fig. 286. A protoxylem element from the stem of *Psilotum nudum* showing a major helical thickening and a secondary-secondary wall outlining simple pit-like structures. × 450. Fig. 287. A helical element from the stem of *Michelia fuscata* showing pits in the tracheary wall between the gyres. × 450. Fig. 288. Section through the protoxylem of the stem of *Liriodendron tulipifera* showing pit pairs in sectional view between parenchyma cells and a helical element. × 450. Fig. 289. As Fig. 287, but *Liriodendron tulipifera*, × 450.

double wall on which can be seen the apertures of elongate bordered pits and the superimposed pattern of simple pits of an adjacent parenchyma cell. The widths of the simple pits were nearly, but slightly less than, the same as the widths of the borders of the pits of the tracheary element.

Koernicke (1925) illustrated and described stretched spiral elements of *Polygonum* in which the spiral thickening had pulled away from the rest of the wall. He noted that where the narrow base of the thickening had been attached there was a distinct groove left in the remaining wall. The grooved wall was shown to be of significant thickness as was also a layer outside of this which he presumably considered to be intercellular substance (*see* his Fig. 1). The structural parallel between Koernicke's illustration and the helical element of *Michelia* (Fig. 252) suggests that probably the grooved wall in *Polygonum* was the secondary-secondary wall deposited over the previous wall after the helical thickenings were established.

A structural framework in pitted angiospermous tracheary elements upon which the pits are superimposed can be detected occasionally. This is illustrated in the early and intermediate metaxylem of *Magnolia*. Some of the early metaxylem elements (Fig. 263) show at a focal plane at the outer limit of the wall nearly transversely oriented helical thickenings with a small sheet of extra wall material between each pair of adjacent bars along the edges of the cell. The dotted line in the drawing represents the cell edge. At a focal plane deeper in the cell the thin sheets between the bars disappear (Fig. 264). A very similar situation has been described and illustrated by Warburg (1883) in *Caulotretus* (*see* his Fig. 7). A similar condition is illustrated from the later metaxylem where the wall material between the helical thickenings was more extensive and pits were clear. The details of matching of these pit areas are shown in Figs. 260 and 261 where it can be seen that the simple pits of the adjacent parenchymatous elements are narrower than the opposing opening of the tracheary element. Commonly one observes in pitted elements of angiosperms a coarse irregular to helical thickening on the inside of the wall of a much greater order of magnitude than the so-called " tertiary spirals ". For example, this is readily observed in vessels of various species of *Quercus*. It is not unlikely that at least some such thickenings are indicative of an ancestral wall pattern upon which the pits have been imposed.

Discussion

The terms used today to describe the various types of tracheary elements, i.e. annular, helical, reticulate, scalariform, pitted, etc., are all words of ancient vintage, dating back at least a century and a half and some longer. They have been used by some authors strictly as adjectives and by others as " technical terms ". When used as technical terms ideally they should be stictly defined as closely as possible and be as unambiguous as possible, and if they are of adjectival origin then they should also be in some way descriptive. When used merely as adjectives, they should be used in a manner which conforms to accepted dictionary meanings. The terms under present consideration appeared first in the botanical literature as merely adjectives and gradually and *incompletely* evolved into " technical terms ". Today they are used mostly as technical terms; previous to the middle of the last century they were used commonly as mere adjectives. In many instances it is quite impossible to determine precisely in which of the two general ways a given author is using certain terms. If one reviews the various applications of these terms and similar ones, he is struck by the extremely variable way in which they have been applied resting on, in some cases, incomplete or erroneous observations or faulty interpretations. From the following table it will be noticed that the term " spiral " was frequently applied to the annular element before 1850. This followed the misinterpretation of Link (1843) that the annular element was derived ontogenetically from a spiral element, an idea which has appeared again recently (Engard, 1944). Unstretched simple reticulate elements have frequently been referred to as " spiral " either as an inter-

pretation or a misobservation. Among relatively recent workers there seems to be little agreement as to the range of elements included under "reticulate", "pitted", or "scalariform".

The term "scalariform" is of particular interest because of its history and variable current usage. This term before the turn of the century was used almost exclusively to refer to what is often called today the "scalariformly pitted element". Before the middle of the 19th century it was generally considered to be a specific term under a broader or generic term, "Leiterförmig". The presumed synonyms of leiterförmig were "leisterförmig", "rayé", and "fendu". The German "treppenförmig" was an exact synonym of "scalariform". The generic term "leiterförmig" (and its three synonyms) was used to refer to a wide variety of tracheary elements which in side view presented a ridged, barred, rayed, or ladder-like appearance; in other words, to unstretched annular elements, unstretched simple helical elements, helical elements with forks, helical elements with forks and anastomoses, reticulate elements with transversely elongate openings, and scalariformly bordered pitted elements. As far as could be determined, the generic terms "leiterförmig", "rayé", and "fendu" had no English counterpart and were never accurately translated. The terms "leiterförmig" and "treppenförmig" have nearly identical English literal translations. It is assumed that this is the source of the usage of "scalariform" in the English literature to refer not only to scalariformly bordered pitted elements, but also to various other types of elements of the protoxylem and metaxylem with some sort of barred appearance in side view. There are some exceptions to the general pattern of usage. Rudolphi (1807) referred to slightly elaborated helical elements as "treppengänge". This usage fits the adjectival meaning of the word, but not necessarily the technical meaning which was current at his time. The term "leiterförmig" in more modern German literature (*see* Table below) is used in the specific sense of the original "treppenförmig" or "scalariform" to refer to the scalariformly bordered pitted element. In the modern English literature the only unambiguous usages of the term "scalariform" are in the expressions "scalariform-reticulate" and "scalariformly pitted" and certainly, in the interest of accurate terminology, all other usages should be avoided.

TABLE 1*

The Annular Element	Element with ring bands, ring thickenings or annular thickenings; ringförmig Gefäss; Ring Gefäss; Ringgefäss; ring vessel; cellula annulifera; vasa annularia; vasseau annulaire; vaisseau annelée; annular element; annular vessel; Ringtracheid; Ringfasserzelle.	Baillon, 1882, 1883; Barkley, 1927; Bischoff 1833; Boodle, 1901; DeBary, 1877; DeCandolle 1821; Eames & MacDaniels 1947; Esau, 1953; Fry, 1954; Foster, 1947; Gustin & Sloover, 1955; Gunkel & Wetmore, 1946; Holman & Robbins, 1934; Haberlandt, 1924; Hayward, 1938; Hartig, 1878; Intern. Assoc. Wood Anat., 1933; LeClerq, 1930; Luerssen, 1881; Link, 1843; Molisch, 1920; Molisch & Höfler, 1954; Ogura, 1938; Pratt, 1917; Rudolphi, 1807; Russow, 1872; Schleiden, 1844, 1849; St. Pierre, 1870; Scherer, 1904; Scott, 1949; Stover, 1951; Strasburger et al., 1908; Tschirch, 1889; Wiesner, 1898; Weis, 1878; Zimmermann, 1930, 1959.

*A summary of the terminology used to describe types of tracheary elements. The terms in the left-hand column are those used in the present study. The ones in the middle column are those which have been applied in the past. They are listed in synonymous groups, except for a few miscellaneous categories. Allowances must be made for the facts that in the earlier literature no distinction was made between tracheids and vessel members, that often the individual cellular components in a vertical series were not recognized, and that in some instances an author was not aware of the existence of a primary wall and thought only of the thickening bands.

TABLE 1 — *contd.*

	Falsche spiral Gefäss, fausse-trachée	Brisseau-Mirbel, 1815; Treviranus, 1806.
	Vaisseau fendu	Brisseau-Mirbel, 1815.
	Ringgerfäss or vasa annularia as a sub-type under Spiralgefäss or Spiroid.	Unger, 1846, 1866.
	Trachée spireau, vaisseau spireau	Slack, 1834.
	Ringförmig Spiralgefäss, vasa spiralia annularia, vasseau spiraux annulaire.	Bischoff, 1833.
	Vaisseau rayé	Bischoff, 1833
The Helical Element (Simple type)	Spirally thickened element; spiral element; element with spiral bands; Spiralgefäss; Spiral Gefäss; spiral tracheid; spiral vessel; cellula spirifera; trachée ou vaisseau spireau; vasa spiralia; vasseau spiraux; vasseau spiralée; Spiralfasserzell; spiral tube.	Atkinson, 1894; Baillon, 1882, 1883; Barkley, 1927; Bischoff, 1833; Bower, 1923; Boodle, 1901; Booth, 1933; Buchholz, 1933; Chrysler, 1937; Crafts, 1943; DeCandolle, 1821; Demalsy, 1953; De Bary 1877; Eames & MacDaniels, 1947; Esau, 1953; Ford, 1902; Foster, 1947; Fry, 1954; Gustin & Sloover, 1955; Hartig, 1878; Holman & Robbins, 1934; Hayward, 1938; Haberlandt, 1924; Int. Assoc. Wood Anat., 1933; Jeffrey, 1917; Luerssen, 1881; Link, 1843; Lestiboudois, 1840; LeClerq, 1930; McNicol, 1908; Meyen, 1830; Ogura, 1938; Penhallow, 1907; Pool, 1929; Pratt, 1917; Rudolphi, 1807; St. Pierre, 1870; Schleiden, 1844, 1849; Scott, 1949; Sifton, 1920; Slack, 1834; Stover, 1951; Strasburger et al., 1908; Treviranus, 1811; Tschirch, 1889; Unger, 1866; Von Mohl, 1839; Weiss, 1878; Wiesner, 1898; Zimmermann, 1930, 1959.
	Helical element, helicule.	Bischoff, 1833; Esau, 1953; Gunkel & Wetmore, 1946.
	Wahr Spiralgefäss	Bischoff, 1833; Treviranus, 1811.
	Trachée, trachea	Bischoff, 1833; Brisseau-Mirbel, 1815; Grew, 1682; Malpighi, 1675.
	Einfach Spiralgefäss, vasa spirilia simplicia	Bischoff, 1833; Unger, 1846.
	Schraubengefäss, Schraubengäng	Bischoff, 1833; Molisch, 1920; Molisch & Höfler, 1954; Russow, 1872; Scherer, 1904; Strasburger, 1891; Unger, 1866; Weiss, 1878; Wiesner, 1898.
	Spiroid	Link, 1839; Schleiden, 1844; Weiss, 1878.
	Vasa adducentia spiralia, v. chymifera, v. hydrogera, vasseau elastique	Bischoff, 1833.
	Air vessel, vasa pneumatochymifera, v. pneumatophora.	Bischoff, 1833; Grew, 1682; Malpighi, 1675.
The Helical Element (with close spirals, some forks and few anastomoses)	Scalariform element, scalariform protoxylem cell, Treppentracheid, Treppengäng.	Barkley, 1927; Booth, 1933; Chrysler, 1937; Eames & MacDaniels, 1947; Esau, 1953; Foster, 1947; Hayward, 1938; Jeffrey, 1912; Rudolphi, 1807; Sifton, 1920; Zimmermann, 1930, 1959.
	Cellula retifera	Schleiden, 1849.
	Vasseau rayé	St. Pierre, 1870.

TABLE 1 — *contd.*

	Vaisseau annelé-reticulé	Baillon, 1883.
	Spiral element with reticulate ramifications	Pool, 1929.
	Spiralgefäss, spiroid	Lestiboudois, 1840; Link, 1843.
	Spiral-reticulate	Baillon, 1882.
	Spiral grades into reticulate	deBary, 1877.
	Element with complex spirals	Crafts, 1943.
	Netzgefäss	Tschirck, 1889.
The Simple Reticulate Element	Spirally thickened element; spiral tracheid, spiral vessel, Spiralgefäss.	Faull, 1901; Ford, 1902; Lange, 1891; McNicol, 1908.
	Reticulate tracheid, cellula retifera	Atkinson, 1894; Schleiden, 1849.
	Treppengäng, finely scalariform element, protoxylem scalariform element, scalariform element.	Boodle, 1901; Eames & MacDaniels, 1947; Esau, 1953; Gwynne-Vaughan, 1901; Hayward, 1938; Rudolphi, 1807; Sifton, 1920.
	Netzformig Spiralgefäss or vasa reticulata as a sub-heading under Spiralgefäss.	Unger, 1846, 1866.
	Treppenförmige Zelle (which on stretching have appearance of netted cells).	Warburg, 1883.
The Reticulate Element (Metaxylem type, includes irregular to scalariform-reticulate)	Netzgefäss, cellula retifera, netzförmig Gefäss, vasa reticularia, vaisseau reticulaire, vaisseau reticulé, Netztracheid, reticulate element, Netzfasserzelle.	Baillon, 1882; Bischoff, 1833; Booth, 1933; Bower, 1923; DeBary, 1877; Eames & MacDaniels 1947; Esau, 1953; Foster, 1947; Heberlandt, 1924; Hartig, 1878; Hayward, 1938; Jeffrey, 1917; Lange, 1891; Link, 1842, Luerssen, 1881; Molisch, 1920, Molisch & Höfler, 1954; Pool, 1929; Pratt, 1917; St. Pierre, 1870; Schleiden, 1849; Scott, 1949; Stevens, 1911; Stover, 1951; Strasburger, 1908; Von Mohl, 1842; Zimmermann, 1930.
	Spiral Gefäss, Spiroid	Link, 1839; 1843.
	Falsch Spiralgefäss, fausse-trachée, falsch luftgefäss, vasseau spiraux faux, vasa spiralia spuria.	Bischoff, 1833; Brisseau-Mirbel, 1815; Slack, 1834; Triviranus, 1806.
	Netzförmig Spiralgefäss, vasa spiralia reticularia, vasseau spiraux ramifié et reticulé, or vasa reticulata as subheading under spiral Gefäss.	Bischoff, 1833; Unger, 1846, 1866.
	Vasseau rayé	Slack, 1834.
	Pitted element	Holman & Robbins, 1927, 1934; Lestiboudois, 1840.
	Irregular netted or pitted element	Cheadle, 1953.
The Scalariformreticulate Element	Vasseau rayé	Baillon, 1882; Slack, 1834.
	Treppengefäss, Treppengang, vasa calariformia, vasseau scalairé, scalariform element.	Bischoff, 1833; DeBary, 1877; Holman & Robbins, 1927, 1934; Smith & Kersten, 1942.
	Tube fendu	Bischoff, 1833.
	Leiter-oder leisterförmig verdicktes Gefäss, Leitergefäss.	Tschirch, 1889.
	Scalariform-reticulate element	Bailey, 1949; Chrysler, 1937; Eames & MacDaniels, 1925, 1947; Esau, 1953.
	Pitted element	Lestiboidois, 1840.

TABLE 1 — *contd.*

The Scalariformly Pitted Element	Spiralgefäss	Link, 1841.
	Treppengang, Leitergefäss, or vasa scalariformia as a sub-heading under Spiralgefäss.	Unger, 1846, 1866.
	Scalariform tracheid, Treppentracheid, Treppengefäss, Treppengang, vasa scalaria, Treppenzelle.	Atkinson, 1894; Baillon, 1882; Boodle, 1901; Bower, 1923; Chrysler, 1937; DeCandolle, 1821; Faull, 1901; Ford, 1902; Gunkel & Wetmore, 1946; Gwynne-Vaughan, 1901; Hartig, 1878; Hofmeister, 1867; Jeffrey, 1917; Lange, 1891; Luerssen, 1881; Ogura, 1938; Rudolphi, 1807; Stover, 1951; Strasburger, 1891; Tschirch, 1889; Von Mohl, 1842; Weiss, 1878.
	Leitergefäss, Leiterförmig Gefäss	Baecker, 1922; Haberlandt, 1924; Luerssen, 1881; Molisch, 1920; Molisch & Höfler, 1954; Russow, 1872.
	Scalariform cell is a loose descriptive term and may refer to a scalariform pitted tracheid.	Eames & MacDaniels, 1947.
	Scalariformly pitted element, scalariform pitted element, Leiterförmig getüpfelt tracheid.	Eames & MacDaniels, 1947; Esau, 1953; Ogura, 1938.
	Vaisseau fendu ou fausse-trachée	Brisseau-Mirbel, 1815.
	Netzförmig Gefäss	Bischoff, 1833.
	Scalariform element as a sub-heading under vaisseau rayé.	St. Pierre, 1870.
	Element with scalariform pitting	In much of the very recent literature.
The Pitted Element (type with more or less circular borders)	Netzförmig Gefäss, vasseau reticulé	Bischoff, 1833; St. Pierre, 1870.
	Netförmig Spiralgefäss	Weiss, 1878.
	Fausse trachée	Slack, 1834.
	Porös spiral Gefäss, vasa porosa, getüpfelt Gefäss, vasa areolata, Tupfelgefäss, Porengefäss, all as subheading under spiral Gefäss.	Unger, 1846, 1866.
	Vaisseau ponctué, Tüpfeltgefäss, Porengefäss, Tupfelgefäss, pitted element, Getüpfelt Gefäss, Punctirt Gefäss, Vaisseau poreaux, Hoftüpfelttracheid.	Baillon, 1882, 1883; Booth, 1933; Brisseau-Mirbel, 1815; deBary, 1877; Eames & MacDaniels, 1947; Esau, 1953; Foster, 1947; Jeffrey, 1917; Lestiboudois, 1840; Link, 1843; Luerssen, 1881; Meyen, 1830; Molisch, 1920; Molisch & Höfler, 1954; Pratt, 1917; Schleiden, 1844; Scott, 1849; Slack, 1834; Stover, 1951; Strasburger, 1908; Treviranus, 1811; Weiss, 1878; Wiesner, 1898; Zimmermann, 1930, 1959.

In the descriptive portions of this manuscript certain terms have been proposed. In all instances the terms were as descriptive as possible, and old established unambiguous terms were given preference over new ones. New ones were proposed only where existing terms did not cover certain new information. The need for a classification of tracheary elements is well brought out by variable terminology in past and present usage, the great variability in the structure of tracheary

elements, and also by the fact that most of the published information on tracheary elements is relatively useless because of inadequate terminology. The following is a summary of recommended terminology to be used in describing certain tracheary elements:

TYPES OF TRACHEARY ELEMENTS — A CLASSIFICATION.

I. *Unthickened elements* (tracheary elements in which there is a primary wall and no secondary wall) (List, 1958).

II. *Annular elements* (tracheary elements in which there is a secondary wall in the form of rings).

A. *Simple annular elements* (annular elements in which the rings are unelaborated and distinct from each other) (Figs. 167, 209, 246).

B. *Directly attached annular elements* (annular elements in which adjacent rings are joined directly to each other) (Bierhorst, 1958; Figs. 8, 9).

C. *Indirectly attached annular elements* (annular elements in which adjacent rings are united by additional strands or sheets of secondary wall material) (Figs. 4, 49, 66, 68; Bierhorst, 1958, Fig. 32).

D. *Reticulated annular elements* (annular elements in which the rings are distinct, but each one is in the form of a reticulum) (Bierhorst, 1958, Figs. 2, 19, 20).

E. *Grooved annular element* (annular element in which the rings are grooved on their inner surfaces).

B-E. Intermediate form between *directly attached annular* and *grooved annular* (where the groove is deep enough to result in some complete doubleness of the rings here and there (Fig. 170).

III. *Helical or spiral elements* (tracheary elements in which the secondary wall is in the form of a helix).

A. *Singly helical element* (helical element in which the thickening is in the form of a single fibrous band).

B. *Doubly helical element* (helical element in which there are two parallel thickening bands).

C. *Multiple helical element* (helical element in which there are a number of parallel thickening bands) (Fig. 128).

D. *Variable multiple helical element* (helical element in which the thickening forks and recombines here and there so that the number of bands at given levels in the cell varies. 1-2 Variable helical element: one in which the variation is from one to two bands within the cell, etc.) (Figs. 126, 127, 172, 190, 191, 207, 212, 220).

E. *Reticulated helical element* (helical element in which the helical band itself has an internal reticulum).

F. *Compound helical element* (helical element in which a number of helical bands are joined to each other by interconnections of secondary wall material to form a single ribbon-form band).

G. *Grooved helical element* (helical element in which the thickenings are grooved on their inner surfaces) (Esau, 1953, Fig. 11.3E).

B-G. Intermediate form between *doubly helical* and *grooved helical* (Figs. 250, 251).

IIA-IIIA. *Annular-helical element* (element which is annular in part and helical in part) (Figs. 24, 26, 109, 117, 125, 138, 139, 169, 177, 199).

IV. *Reticulate elements* (tracheary elements in which the secondary wall is in the form of a network).

A. *Simple reticulate element* (reticulate element in which the network is made up of a system of fine strands; the openings are usually transversely oriented in the unstretched state and irregular to hexagonal in the stretched state) (Figs. 6, 7, 8, 120, 121, 140, 148).

B. *Scalariform-reticulate* (reticulate element in which the secondary wall is relatively massive and in which the openings are in the form of transversely elongate slits with pointed edges).

1. *Edge continuous scalariform-reticulate* (openings in the reticulum cross cell edges) (Figs. 60, 81, 268, 270).

2. *Edge discontinuous scalariform-reticulate* (openings in the reticulum do not cross cell edges).

a. *Trans-edge alternate scalariform-reticulate* (openings in the reti-

culum alternate with each other across cell edges) (Fig. 53).

b. *Trans-edge opposite scalariform-reticulate* (openings in the reticulum fall opposite each other across cell edges, i.e. transverse row of openings continued around a corner) (Fig. 154).

C. *Rectangular reticulate* (openings in reticulum rectahedral). (Only edge discontinuous, trans-edge opposite forms known) (Figs. 35, 36).

D. *Circular or eliptical reticulate* (openings in reticulum relatively large and rounded).

1. *Edge continuous circular or eliptical reticulate* (some of the openings in the reticulum cross cell edges) (Figs. 112, 257).

2. *Edge discontinuous circular or eliptical reticulate* (openings in the reticulum restricted to cell faces and do not cross cell edges; grades insensibly into circular bordered pitted type)

E. *Irregularly reticulate element* (openings in the reticulum of various shapes and orientations) (Cheadle, 1943, Fig. 8; Esau, 1953, Fig. 11.5D).

IIID-IVB 1. *Helical-reticulate* (helical element with forks and anastomoses in the thickening system, but still has a recognizable helical pattern; grades into edge continuous scalariform reticulate) (Figs. 73, 130, 141).

IIA-IVA or IIC-IVA. *Annular-reticulate* (element in which the secondary wall is in the form of a system of rings interconnected by a simple network of thickenings (Fig. 50, lower part; Fig. 69, in part; Fig. 118, in part; Fig. 119, in part).

V. *Pitted* (element in which the openings, either circular, elongate, or semi-elongate or lens-shaped have rounded edges except where crowded or lens-shaped and broad borders except where pits are minute).

A. *Scalariformly bordered pitted* (pits elongate or semi-elongate transversely, more or less).

1. *Trans-edge alternate scalariformly bordered pitted* (pits alternate across cell edges) (Figs. 15, 61).

2. *Trans-edge opposite scalariformly bordered pitted* (pits opposite across cell edges) (Figs. 143, 144, 159).

B. *Oblique and ob-scalariformly bordered pitted* (elongate pits oriented obliquely or vertically) (Figs. 65, 145, 146, 147, 285).

C. *Intra-face rowed pitted* (pits on a given face of the cell falling in rows).

1. *Transversely rowed pitted* (pits in transverse rows) (here are included the pitted elements with opposite and transitional pitting) (Fig. 271).

2. *Obliquely or vertically rowed pitted* (pits in oblique or vertical rows; here are included some of the alternate pitted elements). Under C 1 and C 2: (a) *Trans-edge opposite* . . . (rows of pits continued across cell edges).

(b) *Trans-edge alternate* . . . (rows of pits alternate across cell edges). Under C 1 and C 2: *Tilted axis transversely rowed pitted*, etc. (where the long axes of the pits do not lie along the long axes of the pit rows) (Fig. 155).

D. *Grouped pitted element* (pits on the faces in irregular cluster, sometimes surrounded by rim of Sanio).

E. *Irregularly pitted element* (pits on the faces not in apparent rows or clusters).

F. *Uniseriate bordered pitted* (elements with a single, vertical row of pits on a given face). Corresponds in part with V A1.

1. *Trans-edge alternate uniseriate bordered pitted* (pits alternate across cell edges) (Figs. 12, 13, 206).

2. *Trans-edge opposite* . . . (pits are opposite across cell edges).

The crossing of cell edges by openings in the secondary wall or their restriction to cell faces is certainly related to the establishment of edges and faces during the growth of the cell which is to give rise to a tracheary element. In a tissue in which the cell walls are elastic and in which the cells are enlarging differentially or in which cell divisions are still occurring, the edges and faces of the individual cells are not completely determined. If, for example, two cells A and B with completely elastic walls are situated side by side and separated by a common com-

pound middle lamella, and cell B divides in a plane such that the new cell wall is at right angles to the partition wall, then cell A will bulge out in the direction of cell B such that there will be a separate face in contact with each of the two daughter cells of B separated by a new cell edge. It is assumed that, in the protoxylem, cell edges and cell faces are not yet established at the time when the early tracheary elements determine their pattern of wall thickening and hence the openings do not conform to cell faces. In an annular element when the rings become thickened and lignified, the rings are not circular on their outer edges, but usually strongly angular, reflecting the position of the cell edges to the time when the rings became hardened. They are, however, displaced as the elements are stretched and new cell configurations are assumed by the remaining intact cells.

If trans-edge discontinuous openings are to be expected to form, they should form in the later matured portions of the primary xylem. This is usually the observed case, but there are a few exceptions. In *Angiopteris*, relatively late in the metaxylem one occasionally observes scalariformly bordered pits with their ends slightly crossing the cell edges. Similarly, in *Hibiscus*, lens-shaped pits in the elements of the late metaxylem protrude across cell edges.

Among the vascular plants, one finds various degrees of face conformance of openings in the secondary wall of tracheary elements. Where there is a transition from edge-continuous to edge-discontinuous openings, it often is a gradual one. Such transitions are illustrated by *Lycopodium*, *Angiopteris*, and *Hibiscus*. Hofmeister (1867) noted that elongated pits are usually just as wide as the cell faces.

It is suggested here that pitted elements with trans-edge alternate pitting represent modified reticulate elements in which the points of branching in the network have been shifted so that they fall along the cell edges and hence the openings fall on the faces. This interpretation is based on the transition of cell types found in the primary xylem of *Lycopodium* and in *Angiopteris*, and to a lesser extent on certain members of the Filicales where the elements are only in part trans-edge alternate. Saint-Pierre (1870) spoke of "vasseau rayés" and illustrated one as a helical element with some forks and a few anastomoses. He considered scalariform elements (scalariformly pitted elements) to be modifications of the "vasseau rayés" with superimposed regularity on its faces to become like a ladder. His statement is interpreted to mean essentially the same thing as is stated above, that is a shift in forks and anastomoses toward cell edges. However, this interpretation can only be applied to the trans-edge alternate scalariform elements, namely those of *Lycopodium*, the Marattiaceae, and to a slight extent the Filicales.

Elements with trans-edge opposite pitting are interpreted as representing elements with a basic framework in the form of a helix (simple or complex), or in the form of rings, or in the form of a reticulum in which the openings are elongate and cross cell edges. Opposite pits across cell edges would therefore have the same interrelationship as rowed pits within the faces. Such opposite pits, or in a broader sense rowed pits, are considered to have developed within the same primary pit area. Often the groups are outlined by the "bars" of Sanio as pointed out by Bailey (1919) who also regarded opposite pits as falling in the same primary pit area.

The term "pit area" when applied to tracheary elements, especially primary ones, must necessarily be used in a somewhat looser sense than when applied to thin-walled parenchyma cells. In the latter case they are well known structurally. In the former case they are poorly known, often defined only in terms of the "rims of Sanio" (*see* Bailey, 1919; Sifton, 1920). Esau (1953), who refers her information to Bailey by personal communication, states that pits may or may not be found over primary pit fields. When they are found over the fields, one or more pits may form over a single field. Similarly, pits may arise over primary wall parts that bear no primary pit fields. Esau (1953) states that "thus, there is no absolute interdependence between the position of the primary pit fields in the primary wall and the development of pits

in the secondary wall." The term " primary pit area " as used in the text above is used in a sense to denote an area over which the tracheary element has the potentiality of producing a pit as the result of differential secondary wall formation.

The term " sister pits " is introduced to apply to pits which may be referred to the same pit area. Here would not only be included the rowed pits, but also clustered pits as described by Bailey (1933) in *Cedrus*. The term " singleton " pits is similarly proposed to refer to pits where each one corresponds to an entire primary pit field.

A consideration of circular bordered pits and how they might have evolved seems apropos. In the genus *Lycopodium*, circular bordered pits are to be found in the early metaxylem and occasionally throughout the metaxylem to the exclusion of scalariformly bordered ones. The uniseriate trans-edge alternate arrangement of the pits, either circular or scalariform, and the transition of cell types from simple reticulate suggests only one possible interpretation, this being that the pits are all singleton pits and that in this genus the circular bordered pit is at the same level of phylogenetic specialization as is the elongate pit. In other words, the difference between the two kinds of pits is one of size only.

In the angiosperms, and certain fossil orders, it seems, as has been concluded on numerous occasions, that in most of the woody genera the circular pit has evolved as the result of a " breaking up " of elongate pits into a number of smaller ones. For a full account of the evidence see Frost (1931), Metcalfe & Chalk (1950). This interpretation seems at present too well documented to dispute.

That circular bordered pits are derived by the breaking up of scalariform pits has also been said of the Cordaitales (Bailey, 1925), a conclusion which seems justified as it is in the angiosperms. This conclusion has, however, been extrapolated to probable phylogenetic derivatives of the Cordaites, namely the Conifers, Taxads, *Ginkgo*, *Ephedra*, *Gnetum* and *Welwitschia*. In these extant plants, circular bordered pits appear in protoxylem elements between the kinds of thickenings which are more characteristic of protoxylem elements in general. In the transition of tracheary element types in the primary xylem of these plants, pits become more numerous, the openings in the secondary walls other than the circular bordered pits gradually fill in, in some cases both centripetally and tangentially, and eventually toward the end of the series the elements appear to have circular bordered pits in an otherwise continuous secondary wall. No scalariform or transitional or opposite pitting is to be found. Bailey (1925) interprets the circular bordered pits which occur here as having originated phylogenetically from scalariform pits by the familiar " breaking up " process, and, in the case of those occurring early in the series, as having worked back into the protoxylem and resulted in the elimination of typical scalariform and transitional pitting.

In *Botrychium* and *Helminthostachys* in the Ophioglossaceae one finds circular bordered pits appearing in the protoxylem elements. A transition of cell types follows in the later protoxylem and metaxylem culminating in, as in the gymnospermous plants mentioned above, a pitted element. Nowhere in the transition is there any suggestion of scalariform or transitional pitting. In *Ophioglossum*, however, in addition to the pits appearing in the protoxylem elements, one finds a succession of elements in the late protoxylem and metaxylem showing scalariform-reticulate and finally scalariformly pitted structure. There is no tendency for the scalariform pits to " break up " in the late metaxylem and form transitional or circular bordered pitting. In *Marattia*, one also finds a reticulate to scalariformly pitted transition, and in addition an occasional circular bordered pit in the reticulate elements. It is contended that in the Ophioglossaceae the circular bordered pit originated phylogenetically in the protoxylem or early metaxylem in ancestral forms in which there was in the later formed primary xylem a transition to scalariformly pitted element and that in *Botrychium* and *Helminthostachys* this transition was eliminated and replaced by a transition based on the elaboration of the pitted protoxylem elements.

In view of the existence side by side of these two types of transition in *Ophioglossum* and to some extent in *Marattia*, and the lack of evidence of pits " breaking up " in these genera, it seems justified to infer that the circular pits which appear in the early xylem elements of conifers, taxads, *Ginkgo*, *Ephedra*, *Gnetum*, *Welwitschia*, and also *Equisetum* (*see* Bierhorst, 1958) as well as the Ophioglossaceae evolved in the early xylem as circular bordered pits and not by way of scalariform bordered pits in the metaxylem.

Evidence for the existence of a structural framework in certain pitted elements upon which the pits are imposed is discussed above under the higher Filicales. A definite three-dimensional arrangement of pits in pitted elements where all faces are considered has long been recognized. Link (1839-43) recognized spiral structure and pit arrangement in a variety of types of tracheary elements. Similar recognitions were made by Hartig (1878), Luerssen (1881), Sanio (1863), Record (1925), and Alexandrov (1926). Ontogenetic transformation of a helical type tracheary element into a pitted type was suggested by Hartig (1878) and described in detail in terms of patterns of lignification by Alexandrov (1926) in *Ficus* and *Morus*. In the present paper a similar process is described for *Pteridium*.

Record (1925) states that alternate pits are arranged spirally while scalariform pits are in horizontal series. He interprets that opposite and scalariform pits are developed within an annular pattern. The transverse orientation is, however, no real criterion, since spiral thickenings may be essentially transversely oriented on a given face. Both Record (1925) and Jeffrey (1917) suggest a kind of merging of portions of spirals in the evolution of scalariformly pitted elements. Jeffrey (1917) suggests that from the spiral tracheid " by accentuation of the condition of approximation, fusion between bands results and we have as a consequence the presence of scalariform or reticulate tracheid". This interpretation can be accepted in part. It can possibly be accepted to a certain extent for application to the Marattiaceae, and Lycopodiaceae but to a much lesser extent for application to the Filicales and angiosperms. Jeffrey's interpretation can be applied without contradiction only in the case of scalariform elements which exhibit trans-edge alternate pitting. In the Filicales and angiosperms,[3] scalariformly pitted elements are mostly trans-edge opposite and where a basic helical pattern is discernible, it seems that the helical thickenings do not join directly between the elongate pits, but are united by extra secondary wall material. In other words, the helical thickenings are just as far apart where a pit is present as where one is absent in a given element.

Jeffrey's (1917) interpretation seems more applicable in the case of angiosperm reticulate elements than in the case of angiosperm scalariformly pitted elements. The transition of elements from helical to reticulate, which is mentioned by Weiss (1878) and Zimmermann (1930), along with the details of structure of certain types of reticulate elements indicates that many types of angiosperm reticulate elements may represent modified helical elements in which adjacent gyres are frequently joined as stated by Jeffrey. It follows that the trend to " approximation " and " fusion between bands " is expressed to a much greater extent in the intermediate members of the ontogenetic sequence (the reticulate members) than in the later members (the scalariformly pitted members) within some angiosperms and also possibly in some filicalean ferns. A high degree of reticulation (" approximation " and " fusion ") probably does not occur even in the metaxylem of certain angiosperm families, e.g. Magnoliaceae and Commelinaceae. But again, this statement must be tested by future survey types of studies.

The observations and interpretations presented here emphasize the importance of restricting the concept of the primitiveness of " opposite pitting " over " alternate pitting " to those plant groups in which the conclusion is documented, namely the angiosperms. The same can be said of the primitiveness of scalariformly bordered pits over circular bordered

3. This generality may break down after this feature is looked for in more angiosperms.

pits. The interpretation that there is a phylogenetic trend from scalariform pitting to transitional pitting, to opposite pitting, and finally to alternate pitting (Bailey & Tupper, 1918; Brown, 1918; Frost, 1931) within the angiosperms is particularly well supported by the studies of Frost (1931). Following this interpretation, opposite pits must be regarded as sister pits, that is as having developed within the same pit area. This cannot be said of the apparently opposite pits which appear in the early metaxylem of *Pinus*. In many of the " lower vascular plants " circular bordered pits probably arose phylogenetically independently of scalariformly bordered pits, e.g. Ophioglossaceae, Equisetaceae, Conifers, Taxads, Ginkgoaceae, Gnetaceae, Ephedraceae, and Welwitschiaceae. Similarly, in several groups there is a range in pit size and shape from circular bordered to scalariformly bordered forcing one to infer that all pits in the range are at the same stage of phylogenetic specialization, e.g. *Lycopodium* and possibly *Psilotum*. The major difference between " alternate " and " opposite " pitting within the angiosperms is in the angle of the pit row with regard to the axis of the cell. (*see* Fig. 22 in Moseley, 1948, showing " alternate pitting " in *Casuarina*). Sifton (1920) concluded that in Cycads opposite and alternate pitting may be directly derived from scalariform pitting; this he based on orientation of the pit rows as compared to that of the scalariform pits. Bailey (1925) made a similar suggestion. The range in orientation of scalariform pits includes everything from transverse to vertical, often in the same plant. There is no evidence to indicate that phylogenetic changes in angle of orientation of scalariform pits or rows of shorter pits may not take place in both the direction of the horizontal as well as the vertical.

In certain fossil lycopods, vertical strands of cell wall material (the so-called " Williamson's striations "; *see* Duerden, 1933; Fry 1954; Barghorn & Scott, 1958) have been described as occurring between the larger transverse bars of wall material separating the scalariform openings. These strands have been variously interpreted. Two of the interpretations are: (1) that they represent secondary wall material (Duerden, 1933; Fry, 1954); and (2) that they represent primary wall material (Barghorn & Scott, 1958). For other views reviewed *see* Duerden (1933). The occurrence of minor vertical strands of cell wall material between major more or less transversely oriented strands of wall material is of widespread occurrence among vascular plants. In the Equisetaceae, they occur between annular thickenings (Bierhorst, 1958). Similarly, in the Ophioglossaceae, they occur between annular thickenings, but less regularly disposed and in fewer numbers than in *Equisetum*. Barghorn & Scott (1958) pointed out a condition similar to *Lepidodendron* and related forms in at least one extant angiosperm. There are instances in the Ophioglossaceae and Pinaceae where fine strands of wall material are inserted on a thin border of a bordered pit. The fine vertical thickenings of the Ophioglossaceae and Equisetaceae are, moreover, often of approximately the same dimensions as those in the fossil lycopods. Barghorn & Scott (1958) have insisted dogmatically that the Williamson's striations of fossil lycopods are a part of the primary wall. Their major reason for stating so is the apparent absence of lignin in the fine strands and the presence of the same in the major transverse thickenings which he has designated as secondary wall. It is quite clear, now, that a workable general concept of the primary as opposed to the secondary wall must in the interest of continuity be divorced from any consideration of lignification. Barghorn was apparently quite influenced by statements such as appear in Preston (1952) to the effect that the major chemical difference between the primary and the secondary wall is the presence in the latter and the absence in the former of lignin. Preston in all probability was referring to the primary wall as it was in the growing cell and not to the primary wall as it might be in older cells. Even the primary walls of protoxylem elements may after the period of elongation become quite lignified. Some readers may consider this statement contradicted by the generalization that the protoxylem elements lose

their living contents before elongation and therefore would not be expected to be able to synthesize more wall constituents. The generalization is, however, quite false. If it is at least partly true, it must be so of only early protoxylem elements and of only certain taxa. By a comparison of the Williamson's striations to similar structures in other vascular plants and by accepting the evidence of Fry (1954) from his electron microscope photographs that the strands are intimately connected in their submicroscopic framework to that of the major transverse bars, the interpretation that these are of secondary wall material comes quite naturally.

The dangers of relying on evidence from isolated sources such as single tissues or single organs to support phylogenetic conclusions are well known. These have been brought out in several publications by Bailey (e.g., 1953). Even so, it is always tempting to compare various plant groups with respect to isolated specific characteristics. If conclusions derived therefrom are to a certain extent in accordance with similar ones derived by using other very different kinds of evidence, then the probability of their correctness is greatly increased. With this in mind the following tentative conclusions have been reached. In terms of the structure of the primary tracheary elements:

(1) The living genera of Lycopods (*Lycopodium*, *Phylloglossum*, *Isoetes*, and *Selaginella*) are all phylogenetically relatively remote from each other. This conclusion has certainly been reached on numerous other occasions and is well supported by fossil record as well as comparative morphology.

(2) *Isoetes* is more like *Selaginella* than either one is like *Lycopodium*. This conclusion is based primarily on the presence in the first two genera of simple annular and simple helical elements as well as the reversed helical element, and conversely their absence in the last mentioned genus. This conclusion is in conformity with systems of classification in which the ligule is considered of prime importance.

(3) *Phylloglossum* and *Isoetes* are both specialized forms. This is certainly a generally accepted conclusion. Text descriptions will suffice as support.

(4) The two genera of the Psilotaceae (*Psilotum* and *Tmesipteris*) are quite closely related. Very few and relatively minor differences are to be found between the two genera in terms of their tracheary elements. Recent trends to erect two separate families (Pichi-Sermolli, 1959) seem quite unjustified.

(5) The Psilotaceae is remote from all other extant vascular plants. This is well supported by the peculiarities of their early annular and helical elements as well as the peculiar reticulate elements which appear later in ontogeny.

(6) The Equisetaceae is remote from all other extant vascular plants. See the descriptions of the tracheary elements in Bierhorst (1958).

(7) The three genera of the Ophioglossaceae (*Botrychium*, *Helminthostachys* and *Ophioglossum*) are closely related and form a uniform taxonomic group. This is based on the numerous characteristics of the protoxylem which they have in common.

(8) The three genera of the Marattiaceae studied form a uniform group; *Marattia* being more like *Danaea* than either of the two is like *Angiopteris*.

(9) The two genera of the Osmundaceae (*Osmunda* and *Todea*) are very close. The Osmundaceae in terms of its protoxylem is the most distinctive family among the leptosporangiate ferns.

(10) In terms of tracheary element structure, the Osmundaceae stands in a position intermediate between the higher leptosporangiate ferns and *Angiopteris* in the Marattiaceae.

(11) A fern with tracheary elements rather similar to those of *Angiopteris* may have given rise to the known Marattiales, the Ophioglossales and the Osmundaceae.

(12) If Cycads are genetically related to any of the living fern groups, their origin must be assumed from a level below the Ophioglossaceae and the Marattiaceae. There is no consideration here of whether or not the Cycads evolved from ferns by way of the Pteridosperms.

(13) Cycads show little or no relationship to *Ginkgo*, conifers, taxads or the "Gnetalean" genera.

(14) *Ephedra*, *Gnetum* and *Welwitschia* form a natural group, more closely inter-

related than any one of the three is related to any other known vascular plant.

(15) The taxads are relatively close to the conifers. The taxads and conifers are more closely related to each other than either one is related to any other group of known vascular plants.

(16) The group, *Ephedra, Gnetum, Welwitschia, Ginkgo*, taxads and conifers, is a natural taxonomic unit, and of monophyletic origin.

(17) Angiosperms probably did not arise from known Eusporangiate ferns.

(18) Angiosperms probably did not arise from conifers, taxads, *Ginkgo* or the Gnetales.

Summary

The early-formed tracheary elements of a variety of vascular plants have been described. The range in variation to be found among elements which have been categorically known as "annular", "helical", "reticulate", and "scalariform" is much more extensive than was formerly thought. Many of the specific variants are relatively specific for certain taxa. Several tentative phylogenetic speculations have been presented based on the occurrence of these variants. It has been found necessary to introduce a number of new terms because of new information and also because of ambiguities and variable usages in the previously published literature. A classification of tracheary elements has been formulated in which a minimum of new terms is utilized. The concept of the primary cell wall in terms of stretchability is strongly supported. The flowering plants were barely considered in this study; however, the study strongly indicates that critical survey type studies of the primary xylem elements within the angiosperms should prove extremely rewarding and valuable.

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